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THE BOTANICAL REVIEW

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PLACENTATION IN ANGIOSPERMS

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INTRODUCTION

In these days of rapid progress it is perhaps profitable to have an occasional inspection of our botanical definitions and generalizations. Placentation in angiosperms is a good topic for such inspection. Not only is there some confusion regarding the use of different terms, but our knowledge of the various modes of placentation is rather superficial, acquired, as it was, at a time when little was known about the anatomy of the flower. During the past 60 to 70 years the study of floral anatomy has made notable contributions toward a better understanding of the flower, and it appears to the author that it offers more reliable and better criteria than those hitherto used for distinguishing and defining different types of placentation. Apart from this, placentation has recently been made the basis of a new system of classifying angiosperms into Phyllosporae and Stachyosporae. It will be worthwhile to see how far this division is well founded.

[1] The subject matter of this paper was collected while the author was on a study tour in U.S.A. during 1949–50. A brief outline of the work was presented before the Morphology and Anatomy Section of the VII International Botanical Congress at Stockholm in July 1950.

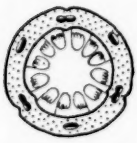
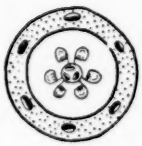
TERMINOLOGY

The term " placenta " has perhaps been borrowed from zoology, but its exact implications are slightly different here. While in animals it refers to the place in the wall of the oviduct to which the foetus or embryo is attached, in plants it means the place or structure on which the ovules (or sporangia) are borne. Generally it is a cushion-shaped structure situated along the line of fusion of carpellary margins. It may be only a swelling of carpellary margins or it may be more or less a distinctive structure, as in the Thymelaeaceae (Heinig, 1951), Solanaceae, Cucurbitaceae and others (Leinfellner, 1951). A perusal of the literature on the subject reveals that the term is used in two senses. Some authors (Wood, 1845; Le Maout and Decaisne, 1876; Hagerup, 1939; Lindsey, 1940; etc.) consider that part which pertains to one carpellary margin as a placenta. According to this view there will be twice as many placentae in an ovary as the number of carpels. Others have used the term for the entire structure situated where carpellary margins meet and fuse (Brown, 1840; St. Hilaire, 1847; Balfour, 1854; Sachs, 1882; Belzung, 1900; Goebel, 1905, 1933; Kratzer, 1918; Mottier, 1932; Warming and Potter, 1932; Puri, 1941, 1942; Eames and MacDaniels, 1947; etc.). This implies that, as a rule, there are just as many placentae as the number of carpels and that each margin bears only half a placenta. Although the point at issue is not of much consequence, yet to a " science which prides itself upon precision of language, any confusion in terms is a reproach ". We must, therefore, use the term in only one sense.

The present author is inclined to follow the lead given by Robert Brown (1840) more than a hundred years ago, in considering each placenta as composed of two half-placentae borne on contiguous margins of the same or different carpels. He wrote (Brown, 1840, p. 556) : " The placenta then of a simple ovarium in its usual state, according to this view, is necessarily double ". No doubt in some cases each half placenta is quite distinct and separate from the other. In certain Orobanchaceae, for instance, the four half-placentae are more or less distinct from one another, and have been interpreted as full placentae (Hagerup, 1939; Tiagi, 1951). But it must be admitted that such individuality of half-placentae is more often lost than maintained.

TABLE I

COMPARISON OF TERMS AS APPLIED BY VARIOUS AUTHORS TO SIX TYPES OF PLACENTATION

	SACHS 1882	VAN TIEGHEM 1891	VINES 1896	ASA GRAY 1879	DUTTA 1933
	Marginal-Apocarp	Axile	Marginal	Parietal	Marginal
	Marginal-Parietal	Parietale	Parietal	Parietal	Parietal
	Marginal-Axile	Axile	Axile	Axile	Axile
	Laminar	Diffuse	Superficial	Superficial	Superficial
	Axial-Lateral	Centrale	Axial Free-central	Free-central	Free-central
	Axial-terminal	Basilaire	Axial basal	Basal	Basal

That each placenta is a double structure appears to be borne out by its vascular supply. It is common knowledge that in the majority of cases every placenta, conceived in this broad sense, receives only one bundle formed by the fusion of two ventral bundles belonging to two carpellary margins. Different stages in the fusion of these two ventral bundles have been recorded. In some cases the double nature of the placental bundle may not at all be obvious, the fusion having taken place in phylogeny (see Smith, 1928; Chute, 1930; Eames, 1931). If each half were a complete placenta, its vascular supply would be more distinct than it usually is. The anatomy of the placental region, therefore, fits better with the Brownian conception of the placenta than with the other.

The two halves of a placenta are generally easily distinguishable from one another, partly on account of a narrow vertical sterile area separating the two halves and partly on account of the fact that the ovules on the two halves are generally oriented in opposite directions. As already pointed out (Puri, 1950), these features have sometimes been overlooked, and queer interpretations have been offered of some placental peculiarities in certain species of the Capparidaceae (Raghavan, 1939; Raghavan and Venkatasubban, 1941).

The more common terms used by different authors are shown in Table I. It will appear from this that Sachs (1882) and some other authors (Zimmermann, 1930; Green, 1904; etc.) distinguish between carpellary ovules and axial ovules (borne on floral axis). It must be pointed out that this distinction involves an interpretation of the morphology of the placenta, which is not yet settled (see last chapter). If our terminology is to be more permanent and lasting it is necessary that it be not based, as far as possible, on views and interpretations which are likely to be changed and modified with time. The terms "axial terminal" for basal and "axial lateral" for free-central, as used by Sachs and others, are therefore unsatisfactory.

Further, Sachs distinguishes the carpellary ovules into "marginal" and "laminar" or "superficial". This treatment has been adopted to a greater or less extent by a number of other authors (Zimmermann, 1930; Wettstein, 1935; Fagerlind, 1946; Troll, 1948; Buxbaum, 1951; and many others). The first of these terms appears to be superfluous, for in the majority of cases the ovules are "marginal" and unless otherwise specified they are

commonly understood to be so. The common terms " axile " and " parietal " do always imply that the ovules are marginal or submarginal. It is, therefore, not necessary—and it is positively inconvenient—to use the compound terms " marginal-parietal " and " marginal-axile ". It is perhaps for this reason that some authors (including van Tieghem, 1891; Vines, 1896; Bonnier et Sablon, 1919; Priestley and Scott, 1949; and almost all American authors) discarded the prefix " marginal " for " axile " and " parietal " placentation.

The condition in a monomerous ovary deserves some attention here. Many authors have distinguished it and described it separately without giving any definite term. Schenk (1884), for instance, in his masterly treatise gives a detailed account of placentation in apocarpous gynaecea and recognizes several variations. Goebel (1933) has followed suit. Some authors, however, have classified the condition as either axile or parietal. While van Tieghem (1891) and some other French authors (Belzung, 1900; Bonnier et Sablon, 1919) have described placentation in the leguminous gynaeceum as axile, Asa Gray (1879) and almost all other American authors following him have classified it as parietal. It is apparent that in calling it " axile " van Tieghem and his followers had in mind the position of the placenta which is situated along the line of fusion of the two margins of the same carpel, while Gray emphasized its apparent peripheral position. It must be pointed out here that this peripheral position is not the same as in a multicarpellary ovary. If we speak with reference to a floral axis it must be admitted that in a monomerous gynaeceum the placenta is borne on the adaxial side of the locule much in the same manner as in axile placentation. Moreover, use of the term " parietal placentation " has been restricted by many non-American authors to a multicarpellary ovary (see Bentham and Hooker, 1912; Jones, 1950). It is, therefore, not proper to describe the condition in monomerous gynaecea as parietal, and perhaps it would be more appropriate if American authors restricted their use of this term to the condition met with in a multicarpellary ovary (cf. Table II).

The designation " axile placentation " is also not satisfactory, for " axile placentation " generally implies a multicarpellary and multilocular condition of the ovary.

It seems logical, therefore, to distinguish between the condition

in a monomerous gynaeceum and that in a multicarpellary one. Gundersen (1939) has emphasized the desirability of such a distinction, but his conception of placentation is slightly different. He writes: " It does not seem desirable to use the term ' pistil ' or ' placentation ' in speaking of plants like *Magnolia, Ranunculus, Rosa,* or *Berberis* with carpels separate or single. For these plants the term ' carpel ' is preferable, thus limiting the word ' pistil ' to flowers with fused carpels. Placentation we consider to relate to the structure of fused carpels only ".

The terminology employed by Dutta (1933) appears to be most satisfactory. He recognizes the condition in the monocarpellary gynaeceum as " marginal " (*sensu restricto*). This term has been used in this sense by a number of authors. For instance, Vines (1896, p. 524) wrote: " in a monomerous ovary . . . the placentation is essentially parietal but it is simply termed ' marginal ' ". Harris and Allen (1919) adopt the same definition and so do Priestley and Scott (1949) and Jones (1950). It has to be admitted that the choice of the term " marginal ", which has been used by many authors (e.g., Sachs, 1882) in a wider sense, is not a happy one. But in the absence of a more suitable term we can perhaps use it profitably provided we keep in mind the narrow sense in which it is used. The main types of placentation as treated here are defined in Table II.

Hitherto the various types of placentation have been defined and distinguished primarily on the basis of the number of loculi in the ovary, and the position of the ovules.

Gynaecea with parietal placentation are unilocular with ovules borne on the periphery, while those with axile placentation are multilocular with the ovules borne on the central column. No doubt these criteria are very practical and handy and have served a useful purpose, especially in elementary studies. But it has to be admitted that for more precise distinction they are not sufficient in themselves, for they are likely to be modified considerably through secondary alterations. Not only are they of little consequence when considered separately, but even collectively they sometimes fail us completely. In *Phaleria* (Thymelaeaceae), for instance, the ovary is bilocular and the ovules are borne more or less in the center, and yet the placentation is described as " parietal " (Heinig, 1951) and perhaps rightly so (Fig. 6). This is explained by assuming the septum as being formed by *inward exten-*

TABLE II

TYPES OF PLACENTATION

Marginal	Axile	Parietal
1. Gynaeceum monocarpellary, apocarpous, unilocular.	Gynaeceum multicarpellary, syncarpous, multilocular.	Gynaeceum multicarpellary, syncarpous, unilocular.
2. Placentae borne on fused margins of the same carpel.	Placentae borne on fused margins of the same carpel.	Placentae borne on fused margins of different carpels.
3. Placentae derive their vascular supply from ventrals of the same carpel.	Placentae derive their vascular supply from ventrals of the same carpel.	Placentae derive their vascular supply from ventrals of different carpels.
4. Ventral bundles inversely oriented with reference to the floral axis and lie almost on the same radii as the dorsals.	Ventral bundles inversely oriented with reference to the floral axis and lie almost on the same radii as the dorsals.	Ventral bundles normally oriented with reference to floral axis and lie on different radii from those of the dorsals.

sion of the two placentae themselves and not by the carpellary margins. Horne (1914) and Wilkinson (1944) have reported a more or less similar condition in certain species of the Cornaceae. The present author is inclined to believe that a multilocular condition of this type, brought about by fusion of the placentae and not of the carpellary margins, is more common than has hitherto been realized (see Junell, 1934). Again, in *Cytinus* (Rafflesiaceae) the ovary is multicarpellary and unilocular in the basal region, and the placental lamellae bearing ovules in bunches on each side project inward. In the upper part of the ovary all the lamellae fuse in the center and result in an apparently multilocular condition (Saunders, 1931) which is, however, different from that in ovaries with typical axile placentation. What is of importance, therefore, is not the number of loculi but how the loculi [2] are produced.

In certain cases the ovary is described as multilocular below and unilocular above. No doubt this is merely a topographical description referring to particular cross-sections without any suggestion that the same ovary can be unilocular in one region and

[2] At one time the author (Puri, 1942) emphasized the need of distinguishing between a "locule"—a cavity enclosed by a single carpel—and an "ovarian chamber"—enclosed by more than one carpel. It seems necessary to distinguish further between a "true" and a "false" locule, the latter being the condition when the cavity is not wholly enclosed by carpellary margins but partly by outgrowths or lamellae from the carpellary wall, as in *Phaleria*, *Cytinus*, crucifers, etc.

multilocular in the other. The placentation in *Parnassia* was long controverted on this account, Lindley (1847) holding it as truly axile and Hooker and Thompson (1858) as decidedly parietal. It was later shown (Arber, 1913) that both observations were partially correct, as they dealt with different regions of the ovary. The same condition prevails in a number of the Tiliaceae (Wiebel, 1948), Sarraceniaceae (Saunders, 1931), Capparidaceae (Puri, 1950), Liliaceae (Eames, 1931, 1951) and many other plants (see Gundersen, 1939). In all these cases it has been taken for granted that in the multilocular region the placentation is invariably axile. As is apparent from the last paragraph, this is not necessarily so. If the multilocular condition is brought about by fusion of placental regions only and not by fusion of carpellary margins (cf. Figs. 1, 2), we are justified in interpreting the placentation as parietal. This makes it inevitable for us to revise our basis for distinguishing between axile and parietal placentation.

Further, the ovary chamber may be partitioned by spurious outgrowths arising from the wall of the ovary or placentae. These spurious septa may divide the ovary transversely, as in *Coronilla* and *Cassia*, or longitudinally, as in *Astragalus* (Baum, 1948), certain Rhoedalean families and some Bicarpellatae, e.g., Boraginaceae, Verbenaceae and Labiatae (see van Tieghem, 1907; Junell, 1934; Wiger, 1935).

Mesembryanthemum and *Punica granatum* present another type of difficulty. The two criteria mentioned above do not go together, that is, while the ovary is multilocular, the ovules are borne apparently on the abaxial sides of the loculi and not in the center as is usually the case (Warming and Potter, 1932; Rendle, 1938; Buxbaum, 1951). In determining the placentation, the peripheral position of the ovules seems to have been considered quite arbitrarily as all important, and the condition has been described as parietal [3] in utter disregard of the multilocular condition. In the opinion of the present author such a condition should be regarded as axile, the ovules being borne on the fused margins of the same carpel, their peripheral position being simply derived (cf. Figs. 3–5).

In *Crataeva religiosa* (Capparidaceae) the gynaeceum is usually bicarpellary, but some tetracarpellary gynaecea have also been re-

[3] Van Tieghem (1891) has described the condition as "median parietal". He evidently means that the ovules are borne on midribs (see next chapter).

ported (Puri, 1950). Of the four carpels occurring in such cases the two median ones are generally smaller. It has been observed that in some of these cases the two median carpels in their basal region enclose distinct loculi of their own and contain their ovules within them. The two lateral carpels, however, which are of normal size, are "open" and together enclose a common cavity running across the center. As a result of this the ovary appears to be trilocular; in certain cross-sections two of the loculi belong to the two median carpels and the third is common to the two laterals (Figs. 7–9). Horne (1914) has described similar cases in certain species of the Caprifoliaceae. It is difficult to have a correct appreciation of such a condition merely on the basis of the criteria so far in use.

Further, the position (peripheral and central) of the ovules also is not a reliable criterion. It may vary considerably in both axile and parietal placentation. In fact in parietal placentation they may no more be peripheral than in a typical axile placentation. A detailed discussion of the position of a placenta will be taken up in the next chapter.

In certain species of the Berberidaceae Chapman (1936) has observed a very interesting condition. Here, on account of the "solidification" of two of the three carpels, the axile placental column has become pushed to one side and the ovary has become unilocular. Such a modified condition is understandable only on the basis of anatomical studies.

In view of these considerations it is desirable that we have our classification of placentation based on more reliable criteria, all the more so if placentation is to play its role as a useful character in taxonomy. The merely topographical basis that has been given to it so far is of little avail and is often misleading. Anatomical studies of the flower have been of considerable help in revealing at least some of the secrets of flower structure (Puri, 1951), and the present author thinks that they can also be profitably employed in a study of placentation. The following three criteria based on anatomical considerations together with the two mentioned above should be taken into account for a scientific classification of placentation [4].

[4] It may be pointed out here that the author does not want to convey the idea that the various types of placentation are fundamentally different from one another. In fact all possible gradations between one type and another are well known.

a) Composition of the vascular supply of a placenta—whether from one or two carpels.

b) Orientation of the vascular supply of a placenta—normal or inversely oriented with reference to the floral axis.

c) Location of the placenta—on the fused margins of the same or of different carpels.

Such a broad basis will no doubt make the task of an elementary student more difficult, but it will certainly impart greater dependability to placentation as a character in taxonomy. It is possible that in some cases the anatomical criteria may conflict with the topographical ones. For instance, in *Forsythia* (Oleaceae), although the ovary is bilocular with axile placentation, the anatomy is apparently that of parietal placentation, the ventral bundles of adjacent carpels having fused in pairs (Fig. 10). This is no doubt an intermediate position, and perhaps it will not be too much to suggest that the axile placentation in this species is on its way to becoming parietal (or vice versa?). The stage is all set; what is required is merely a split through the center of the septum in the direction of the arrows in Fig. 10.

A brief statement of the different types of placentation seems to be called for here.

MARGINAL PLACENTATION (*sensu restricto*). The condition is defined in Table II. It has to be clearly distinguished from the type of placentation met with in pseudomonomerous gynaecea which occur in the Gramineae (Schuster, 1910; Arber, 1934), certain Icacinaceae (Fagerlind, 1945*a*), Cucurbitaceae (Kratzer, 1918; Puri, 1952*b*), Thymelaeaceae (Heinig, 1951) and others (see Eckardt, 1937, 1938; Junell, 1934; Wiger, 1935). In all these cases the placentae are essentially parietal, as they occur at the junction of two margins belonging to different carpels and receive their vascular supply from either one margin or two margins belonging to two carpels (cf. Fig. 13).

AXILE PLACENTATION. The term "axile" should be clearly distinguished from "axial". By some authors (Douglas, 1936; Lindsey, 1940; Gauthier, 1950; Heinig, 1951) the latter has been used for the former. This is unsatisfactory in so far as the term "axial" means that the ovules are borne on the floral axis (see Prantl, 1937) which is actually not implied. Again, Wilson and 'X' (1947) in describing the "flower" in Encyclopaedia Britan-

nica have perhaps inadvertently used the term "axile" for the condition that is commonly described as "free central". They write: "But often the placentae arise from the axis (axile placentation) and are not connected with the carpellary leaves".

Some authors have preferred to use the term "central" for "axile" (Campbell, 1930; Wiger, 1935; Pool, 1940; etc.). This too is unsatisfactory, for the term "central" has sometimes also been used to describe the condition usually labelled as "free central" (van Tieghem, 1891; Belzung, 1900; Bonnier et Sablon, 1919; Sinnott, 1946; Fuller and Tippo, 1949).

PARIETAL PLACENTATION. Our conception of parietal placentation is slightly different from the one commonly held. Emphasis is placed here on the three criteria enumerated above and not so much upon the number of loculi. If the placentae are borne on the fused margins of two carpels we shall describe the placentation as "parietal", even though the various placentae may secondarily cohere among themselves and give rise to a "multilocular" appearance in some region of the ovary (cf. Figs. 1, 2). In other words, if fusion in pairs between half placentae of different carpels is primary and more intimate than that between those of the same carpel, we are justified in describing the placentation as "parietal" (cf. Leinfellner, 1950). It is on such considerations that the condition in the Cucurbitaceae is interpreted as parietal (Puri, 1952*b*). Owing to subsequent hypertrophy the margins of individual carpels may also fuse sometimes and thus create the "multilocular" condition.

Parietal placentation sometimes has been divided into two types, that which is simple parietal and that which is derived from the axile state (Eames and MacDaniels, 1947; Gundersen, 1950). Puri (1945, 1947, 1950) has described a derived type of parietal placentation in a number of Rhoeadalean families and in the Passifloraceae and Cucurbitaceae, but he is not sure that the simple type of parietal placentation actually exists. In this connection the recent work of Bailey and his associates on some of the primitive Ranalian families may be of some significance (Bailey, Nast and Smith, 1943; Bailey and Nast, 1943, 1945; Nast and Bailey, 1945, 1946; Swamy and Bailey, 1949; Bailey and Swamy, 1949, 1951; etc.). On the basis of this extensive work these authors have asserted that the primitive carpel is a conduplicate structure and not

a flat tri-lobed leaf-like organ, as has so far been believed by Sinnott and Bailey, 1914; Eames, 1931; Hunt, 1937; and others. If this is true, then "open" carpels of the type met with in typical parietal placentation would be derived, not primitive. We shall revert to this topic at a later stage.

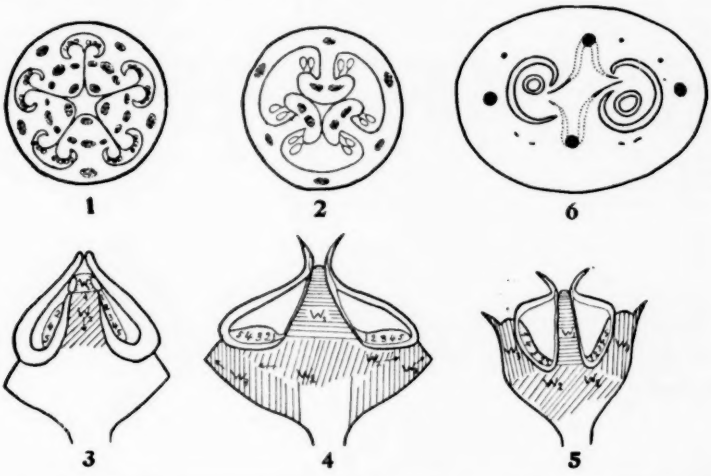
Saunders' conception of carpel polymorphism does not admit of any parietal placentation in the usual sense. According to her the ovules are not borne on carpellary margins but mostly on the so-called reduced "solid" carpels, and hence she concludes that parietal placentation, as commonly understood, does not exist.

FREE CENTRAL PLACENTATION. Although not a very appropriate expression, "free central placentation" has been very widely used for the condition so labelled in Table I. Moss (1920) has preferred to distinguish between "free marginal placentation" and "free central placentation". The former expression he uses for the condition in the Caryophyllaceae where the fused margins break away during development of the gynaeceum, and the latter to the condition in the Primulaceae where the fused margins are separate from the ovary wall from the very beginning. As has already been pointed out (Dickson, 1936), such a distinction is not only superfluous but uncalled for because the condition in the two families is essentially the same.

BASAL PLACENTATION. It is desirable that this term be used for the condition where a single ovule arises or appears to arise from the bottom of the ovary. A really basal ovule in the majority of cases—perhaps in all cases—arises from axile placentation (cf. Eames, 1951). The condition in the Gramineae and certain Ranales, where the single ovule has descended from a lateral position, cannot legitimately be described as "basal". This is either "parietal" or "marginal" (*sensu restricto*), or "sub-basal".

SUPERFICIAL, LAMELLAR AND SEPTAL PLACENTATION. These terms, which have often been used as synonyms, need to be distinguished from one another. When the entire or most of the internal surface of the ovary wall is covered with ovules, as in the Nymphaeaceae and Butomaceae, the condition should be described as "superficial" or "laminar" (Zimmermann, 1930). Sometimes, as in certain species of the Rafflesiaceae and perhaps in some Papaveraceae, the placentae enlarge considerably and extend to-

ward the center. Apparently carpellary margins do not take part in the formation of these inward extensions and as such they are not true septa but merely placental lamellae, and the placentation may be described as merely parietal or lamellar. If, however, there are indications of the carpellary margins also protruding in and forming incomplete septae, and if the ovules are borne all over their surface, the placentation may be described as " septal ".



FIGS. 1 AND 2. Transverse sections through ovaries of *Sarracenia flava* and *Heliamphora nutans*, respectively. Note that, although the ovaries are apparently multilocular, the placentae are parietal. (After Saunders, 1931, who considers the placentae as " fertile carpels ").

FIGS. 3–5. Show the change in position of placentae in *Mesembryanthemum* on account of differential growth. In young condition the ovules are borne in the center, but later they slide, as it were, to the periphery. (After Buxbaum, 1951).

FIG. 6. Transverse section through ovary of *Phaleria*, showing bilocular condition and the two ovules being borne more or less in the center. (After Heinig, 1951, who interprets the placentation as parietal).

POSITION AND VASCULAR SUPPLY OF PLACENTAE

Ovules are almost always borne on the upper (adaxial) side of the carpellary leaf. In the majority of cases they are confined to the marginal or submarginal regions of carpels (Brown, 1840; Troll, 1939; Eames and MacDaniels, 1947; etc.). In a few cases, however, they have been reported to occur on the dorsal side of the

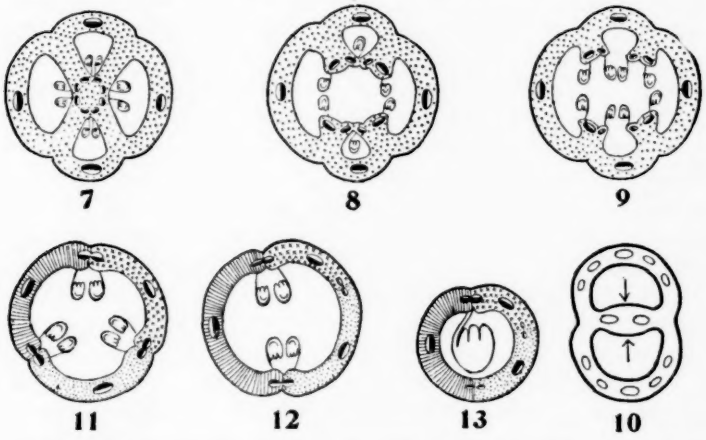
carpellary leaf. Goebel (1905) cites his own earlier work and that of Chauveaud (1892) and of Braun (1874) reporting dorsally borne ovules. Since the correctness of these earlier observations had been questioned by Čelakovsky, Goebel (1905, 1933) reiterated the fact and gave transverse sections of the ovary of *Erythraea pulchella* where the inturned margins of the carpels "bear the ovules on the under surface and upon the margins". Thompson (1934) figures some "emergences" corresponding to ovules within the septal chambers of certain Scitaminaceae. If these are lined by the dorsal epidermis and if the "emergences" are actual ovules, though abortive, it seems likely that the dorsal surface of the carpel is also potentially ovuliferous. A more or less similar conclusion has been arrived at by Lam. Referring to an earlier report by Newman (1928), he writes (Lam, 1948*a*, p. 138): "And if Newman's interpretation of the carpellary leaf margin in the amaryllidaceous *Doryanthes* . . . is correct, it appears that ovules in phyllosporous angiosperms need not necessarily be inserted on the margin or on the upper (adaxial) leaf surface, but that they may be slightly shifted to the lower (abaxial) leaf side as well, provided that their protective inclusion within the infolded carpel is not endangered".

In a few cases, as in the Nymphaeaceae and the Butomaceae, the ovules are scattered nearly all over the inner surface of carpels. Such a condition is difficult to explain, especially for those who believe in the axial nature of the placenta. We shall return to this topic again in due course.

Some cases are on record where the ovules have been described as borne on the mid-ribs of carpels. Almost all such reports have been shown to be incorrect. Van Tieghem (1907) spoke of "dorsal" ovules and "ventral" ovules with respect to their position on the mid-ribs or margins of carpels in the Verbenaceae. In fact he divided the family into two groups on the basis of this character. Unfortunately his statements were not accompanied by any figures. Junell (1934), who has made a detailed study of the gynaeceum structure in the Verbenaceae and the Labiatae and who has profusely illustrated his account, has not come across any dorsally borne ovules, even in those groups which were described to have them by van Tieghem. Junell, therefore, comes to the conclusion that all ovules in the Verbenaceae are borne on carpel-

lary margins. He, however, describes several variations concerning the relative position of the ovule-bearing margins of carpels.

Zygogynum (Winteraceae) was also described as having the ovules on the mid-rib (van Tieghem, 1900). A reinvestigation has revealed, however, that, although the ovules are attached to the abaxial side of the locule, they are borne on a morphologically ventral part of a conduplicate megasporophyll that has been de-



FIGS. 7–9. Transverse sections through a tetra-carpellary ovary of *Crataeva religiosa*, showing four unequal carpels which disappear at different levels. Note that in Fig. 8, while the lateral carpels are "open", the median ones are still "closed".

FIG. 10. Transverse section through ovary of *Forsythia*. Although the ovary is bilocular, the ventral bundles of adjacent carpels have fused in pairs, as they do in parietal placentation. (After Eames, 1931).

FIGS. 11–13. Show how the pseudomonomerous condition is obtained from the multicarpellary condition through sterilization of all but one or only one half of a placenta.

flected into an abaxial orientation and thus overtops the much shortened morphologically dorsal part of the carpel (Bailey and Nast, 1943).

The condition in some species of *Mesembryanthemum* is somewhat similar to that in *Zygogynum*. Here the ovary is multicarpellary and multilocular, but the position of the ovules in advanced stages of development may shift from the center to the periphery (see Figs. 3–5). What happens is that excessive growth of the

peripheral tissue during development gradually turns the locule completely over so that the axile placentae are drawn out, as it were, and lie along the " dorsal suture " (Brown, 1840; Warming and Potter, 1932; Rendle, 1938; Willis, 1948; Buxbaum, 1951; etc.). But it must be borne in mind that in all species of *Mesembryanthemum*, as in *Zygogynum*, the ovules are borne on the morphologically ventral part of a carpel and that we cannot legitimately call the placentation " parietal " as has been done by some taxonomists (Warming and Potter, 1932; Rendle, 1938), even though the ovules may appear to be borne on the periphery [5]. On the basis of the criteria formulated above, the placentation is clearly axile, for the placentae are actually borne on the " ventral sutures " of carpels. Further, the author believes that anatomical studies will support such an interpretation [6].

Punica granatum presents another interesting case. Here the inferior ovary is formed from two whorls of carpels in two tiers. The inner lower whorl generally has three carpels, and the placentae are situated in the inner angles of the three loculi. The external whorl is 5-merous and the placentae have originally the same position in the inner angles of the loculi. But their position is later changed to the outer side of the locule, owing to the growth of the wall of the ovary, which takes place early, causing the carpels to become, as it were, turned inside out so that the part which was turned inward becomes turned outward (Warming and Potter, 1932). For the reason stated above, the placentation here, too, is essentially axile, even though the ovules may come to be situated on the abaxial side of the locule. Mere position of the ovules, therefore, is no safe criterion for distinguishing types of placentation.

With a view to explaining the peculiarities of the placental region of the crucifer gynaeceum, Spratt (1932) postulated an hypothesis that the ovules here are borne on the mid-ribs of carpels. This is based on a misconception. She assumed, for instance, that, like a foliage leaf, a carpel also must have a prominent mid-rib and less prominent lateral veins. Under this assumption, which is quite unsound, she interpreted the bundles in the placental regions

[5] Wettstein (1935) has called such a condition " parietal-laminar " as against " parietal-marginal ".

[6] A study of floral anatomy of the Cactaceae, Aizoaceae and allied families is in progress in this Laboratory.

as mid-rib bundles and those in their places (mid-rib bundles) as ventrals. Recent work (Thomas, 1934; Hunt, 1937; Sprotte, 1940; Puri, 1941; etc.) has shown that, contrary to the condition in a foliage leaf, the ventral bundles in a carpel are generally better developed, perhaps in response to their ovule-bearing function, than the dorsals. This takes away the entire support for Spratt's interpretation. Moreover, the placental peculiarities in the Cruciferae and allied families have been more satisfactorily explained otherwise (Puri, 1945, 1947, 1950).

Ovules, therefore, in the majority of cases are marginal or submarginal, and in no case, as far as could be ascertained, are they borne on the mid-ribs of carpels. By virtue of their position, the placentae receive their vascular supply from the ventral bundles of carpels, a fact clearly recognized as early as 1844 by Brongniart. In many cases, as in the Ranunculaceae, Leguminosae, Rosaceae and Liliaceae, the marginal bundles themselves supply the ovular traces and may thus be called "placental strands". Eames and MacDaniels (1947) do not apparently approve of this expression. They argue that: "In follicles, achenes and some other types of ovaries, the placenta is merely a position and there is no placental supply as such. Where the placenta is a definite, often fleshy enlargement of an area along the margins of the carpel, it is supplied by branches from the ventrals, which branching further, give rise to the ovule traces as in the Ericaceae and Cucurbitaceae". Recent studies in these families, however, seem to indicate that the carpellary ventrals themselves constitute the vascular supply of the placentae (see Palser, 1951; Puri, 1952*b*).

In a few cases the dorsal bundles of carpels may also contribute to the vascular supply of the ovules. This has been reported for some Ranalian families. The condition in *Cabomba* (Nymphaeaceae), which has been worked out in detail by Saunders (1936), is quite interesting. Here, three or four ovules arise from the ovary wall at points about mid-way between the ventral and dorsal mid lines. The mid-rib bundle on entering a carpel immediately gives off a pair of laterals which diverge until they become separated from each other by almost as large an arc of the circumference as that which lies between each of them and the mid-rib. There is thus no single bundle or pair of bundles in the ventral mid line such as characterizes the typical monocarpellary ovary. At the level of origin of the lower pair of ovules a strand is ordi-

narily given off by each of the lateral bundles on the side toward the mid-rib and runs in the ovary wall in a horizontal direction. These strands are met by two corresponding horizontal strands from the mid-rib. It is from these two junction points that the two ovular traces diverge. At the higher level where, as a rule, only one ovule develops, the two laterals converge and, meeting in the ventral mid line, give off the bundle for the third ovule and so come to an end.

In certain species of the Winteraceae (Bailey and Nast, 1945) and in *Trochodendron* (Nast and Bailey, 1945) also the mid-rib bundles may contribute some ovular traces.

In some uniovulate carpels of the Ranunculaceae the ovular trace for the single sub-basal ovule has been observed to arise as a branch from the dorsal (Smith, 1928; Chute, 1930; Eames, 1931). But here the dorsal bundle is interpreted, perhaps rightly, as a compound bundle formed by adnation of the dorsal and the much reduced ventral bundle, and it has been suggested that it is from this latter part that the ovular trace arises (Chute, 1930; Eames, 1931).

The vascular supply of the placental region in certain Rhoeadalean families, particularly in the Cruciferae, has long attracted attention and has been variously interpreted. Though the placentation is often described as parietal, the placental bundles, unlike the placental bundle of an ordinary parietal placenta, are inversely oriented—a condition peculiar to axile placentae. This has been observed in the Cruciferae (Gerber, 1900; Hannig, 1901; Eames and Wilson, 1928, 1929; Arber, 1931; Puri, 1941), Capparidaceae (Puri, 1950), Papaveraceae (Dickson, 1934; Arber, 1938) and the Moringaceae (Puri, 1942), and is believed by some to be an important architectural feature. Besides, such a condition has been observed to occur also in the Passifloraceae (Puri, 1945; 1947) and the Cucurbitaceae (Puri, 1952*b*).

Gerber (1900), who was perhaps the first to observe the inverse orientation of the placental bundles in the Cruciferae, was led to the conclusion that the septal region in this family is formed by two inverted carpels. Hannig (1901) supported this interpretation. Later Eames and Wilson (1928) offered another interesting interpretation of the crucifer gynaeceum on the basis of the inverted placental strands. They suggested that the two placental regions are formed from two median carpels which through re-

duction have lost their loculi and forced their ovules out into the central cavity enclosed by the two lateral, sterile, valve carpels. Thus according to them there are four carpels in the crucifer gynaeceum—two of the lateral sterile and "valve" type and two of the median fertile and "solid" type. They applied the same interpretation to the Capparidaceae (Eames and Wilson, 1928). Dickson (1935) interpreted the condition in the Papaveraceae in a somewhat similar fashion.

At one time the present author (Puri, 1941) also accepted this interpretation with some modification regarding the mode of "solidification" of the median carpels. He further explained the condition in the *Moringa* gynaeceum along similar lines (Puri, 1942). But his recent studies in the Passifloraceae and the Cucurbitaceae have compelled him to withdraw from that position and to offer a different interpretation for the inversion of the placental strands (Puri, 1945, 1947, 1950, 1952*a*). He now holds that there are just as many carpels in the gynaeceum of the Rhoeadalean families as the number of placentae. Inversion of the placental strands is explained thus: In the ancestors of these families the ovary had axile placentation—a condition still seen in certain species of the Capparidaceae, Passifloraceae and Cucurbitaceae. In a change from axile placentation to parietal the placental strands have shifted to the periphery, but they have still retained their inversion so characteristic of axile placentation. Thus the inversion of these bundles is just a relic of past history which has somehow been retained.

Arber does not seem to attach my importance to the inverted condition of the placental strands[7]. She writes (Arber, 1938, p. 661): "The occurrence of 'inverted' bundles in the placenta is only one of the aberrant results that may follow when one collateral bundle has to supply a vascular system for a structure internal to itself on the same radius of the shoot". Eggers (1935) also does not attach any importance to the inversion of these placental bundles. However, as was pointed out earlier (Puri, 1945), it does not appear likely that mere "branching" can permanently alter such an important anatomical character as the orientation of a bundle.

[7] Elsewhere, however, she has considered inversion of bundles as an important structural feature (Arber, 1925, p. 5).

It is common knowledge that placental or ventral bundles do not ordinarily give out any branches to the ovary wall; they confine themselves to the placentae and generally disappear with them. It it equally true that the dorsal bundles and the median ventrals, wherever they exist, play little part in the supply of ovular traces [8]. This independence of the vascular supply of the dorsal system from that of the ventral system is noteworthy. The condition in *Crataeva religiosa* (Puri, 1945, 1950) is even more significant. Here, just below the ovary, the androgynophore possesses two rings of vascular tissue, one within the other. The inner of these, which appears to arise *de novo* and which alone furnishes placental strands, has no connection, at least for some distance above the place of its origin, with the outer ring which supplies other carpellary bundles (see Puri, 1950). A more or less similar condition has been observed in certain species of the Cucurbitaceae (Puri, 1952*b*), Urticaceae (Bechtel, 1921) and Scitaminaceae (Thompson, 1934, p. 15–16).

Such cases can, of course, be used to support the view of "independent blastem" for placentae (see Le Maout and Decaisne, 1876). We shall consider this point in greater detail at a later stage. It may, however, be pointed out here that the condition can be satisfactorily explained by the exponents of the so-called classical interpretation of the gynaeceum. They have only to assume that, phylogenetically speaking, the vascular tissue which supplies the ventral bundles here becomes separated from the rest of the vascular tissue at a very early stage.

The condition in uniovulate or biovulate gynaecea deserves some attention. The adherents of the classical interpretation of the carpel would have us believe that in an ovary with a single ovule only one of the margins of the component carpels is fertile. Ordinarily the "placenta", which is one half in such cases, should receive only one bundle corresponding to a single ventral. Cases are, however, on record where such a half placenta, and the ovule borne on it, receive more than one bundle. In *Juglans regia*, for instance, there are generally two carpels in the ovary and four corresponding ventral bundles in the placental region. All these four

[8] In certain species of the Cucurbitaceae the author has observed that bundles other than the placental strands also contribute to the vascular supply of placentae and ovules.

bundles enter directly into the single ovule which, though apparently basal, has been described as parietal (van Tieghem, 1869*a*; Benson and Welsford, 1909). A similar condition has been reported in *Morus nigra* and *Rheum undulatus* (Benson and Welsford, 1909).

In certain species of the Cyperaceae, too, the vascular bundles, which apparently belong to carpels other than the one which is fertile, also enter the single basal ovule (Blaser, 1941*a, b*). In *Sicyos angulata* (Cucurbitaceae) the unilocular ovary contains a single pendent ovule which receives its vascular supply from three sources, almost equidistant from one another. These three sources are believed to represent three placental bundles of three carpels (Puri, 1952*b*).

In certain species of the Caprifoliaceae the vascular supply of the single ovule present is described as " compound ", being contributed by more than one vascular bundle (Horne, 1914; Wilkinson, 1948*a, b,* 1949). An interesting situation exists in *Viburnum* where the single fertile ovule not only receives " compound " vascular supply but also lies in the loculus of a sterile carpel, other than the one which bears it (Wilkinson, 1948*c*).

Chapman's (1936) observations are also interesting from this point of view. In certain species of the Berberidaceae she has observed certain bundles in the placental region which do not provide any ovular traces. She has been led to believe that these bundles are other than the ventrals and belong to carpels which have become almost pressed out of existence. What has happened to the ventrals of the reduced carpels is not clear.

In *Garcinia livingstonii* the ovary is generally bilocular and each locule contains a single ovule. Here the right h d margin of one carpel supplies the strand for one ovule, and the left hand margin of the other carpel the other ovule. The placental region is thus believed to be composed of only two margins belonging to two carpels (Puri, 1939).

NUMBER OF PLACENTAE

The number of placentae in an ovary is ordinarily the same as the number of carpels. While this correspondence is not of much consequence, any departure from it is obviously of some interest, employed as it may be to support the doctrine of independence of

the placentae from the carpels. It will, therefore, be worthwhile to examine all cases where the placentae in an ovary are fewer than the carpels.

All cases of pseudomonomerous gynaecea are interesting from this point of view. In such instances the ovary is unilocular and has only one (sometimes only one-half) placenta. There are clear indications, both anatomical and morphological, to show that the ovary at such times actually consists of more than one carpel. Placentation in pseudomonomerous gynaecea, however, should be distinguished from marginal placentation in truly monocarpellary ovary. Pseudomonomerous gynaecea occur in many families—in certain species of the Verbenaceae (Junell, 1934), Icacinaceae (Fagerlind, 1945*a*), Cucurbitaceae (Kratzer, 1918; Puri, 1952*b*) Gramineae (Schuster, 1910) and many others (see Eckardt, 1937, 1938).

In some members of the Gramineae there are clear indications of three carpels in the ovary (Arber, 1934), but only one ovule, attached parietally. This shows that only one half of a placenta is fertile. Arber (1929) has reported that in *Bambusa*, in some abnormal cases, two ovules are present, facing right and left. When only one ovule is present, as is the usual condition, it also faces one side, showing thereby that it may be one of a pair. This seems to indicate that a process of sterilization of the placentae is in progress in the ovary of the Gramineae. It is likely that in the ancestral forms all three placentae of the ovary were fertile. In present day forms, however, only one margin of one of the three carpels is fertile, and it bears only a single ovule (cf. Figs. 11–13).

Some significant stages in the pregressive sterilization of carpellary margins have been observed in certain species of the Cucurbitaceae. In *Echinocystis lobata* Kratzer (1918) figures an ovary with three carpels, of which only one is fertile, producing two half placentae. In *Cyclanthera pedata* he reports an ovary with two carpels producing only one placenta. In this case one margin of each carpel is fertile. In *Sicyos* and *Sechium* there is a single pendent ovule. In *Sicyos angulata* the present author has found evidence, both anatomical and morphological, that there are three carpels. If this is so, then in these uniovulate ovaries only one margin of one of the carpels is fertile and the rest are sterile. In this way several stages in gradual sterilization of carpellary mar-

gins can be traced in the Cucurbitaceae. All such cases ultimately lead to the pseudomonomerous condition in which placentation always remains parietal.

In *Crataeva religiosa* (Capparidaceae) the author (Puri, 1950) came across an interesting case. In this particular instance the ovary is biplacental in the lower region, but one of the two valves of the ovary is larger than the other and contains a greater number of bundles. In this larger arc of the circumference of the ovary a third placenta makes its appearance half way up the ovary, which thus becomes triplacental in the upper region. This has been interpreted as indicating sterilization of two of the contiguous carpellary margins in the lower region and seems to have nothing to do with independence of placentae. More or less similar cases have been observed in other members of the Capparidaceae.

It can be safely concluded from the preceding account that there is a close correlation between the number of placentae and that of carpels. Wherever this correlation breaks down it is due to sterilization of some of the carpellary margins.

The vertical extent of a placenta varies considerably. Generally it runs almost along the whole length of carpellary margins in an ovary; only a little of the lower portion and the upper portion may be without ovules. In specialized cases, however, a placenta may bear only one or two ovules, and it may consequently be confined to the basal region of the ovary, as in the Compositae, Polygonaceae, Ranunculaceae, Gramineae, etc., or to the upper region, as in the Umbelliferae, Combretaceae, etc.

EVOLUTIONARY TRENDS IN PLACENTATION

Fig. 14 attempts to show a tentative scheme of the evolution of placentation in angiosperm flower. It is apparent that there is no uniform pattern followed and evolution seems to have progressed along several lines. Nevertheless, free central placentation appears in all cases to have been derived from axile placentation (Brown, 1840; van Tieghem, 1869*c*; Lister, 1884; Bancroft, 1935; Douglas, 1936; Dickson, 1936; Wilson and Just, 1939; Thompson, 1942; Joshi, 1947; Puri, 1951; Eames, 1951). The same can perhaps be said of basal placentation as it exists in the Cyperaceae (Blaser, 1941*a*, *b*), Polygonaceae (Laubengayer, 1937) and other families. The condition in the Gramineae, Compositae and certain

species of *Ranunculus*, though often described as basal, is actually lateral or sub-basal, since it is derived from parietal placentation.

Thus to the followers of the classical interpretation of the carpel, free central and basal[9] placentations are derived types. To those who interpret the placentae as axial structures, such cases are the simplest. For instance, Payer (1857) considered *Polygonum*,

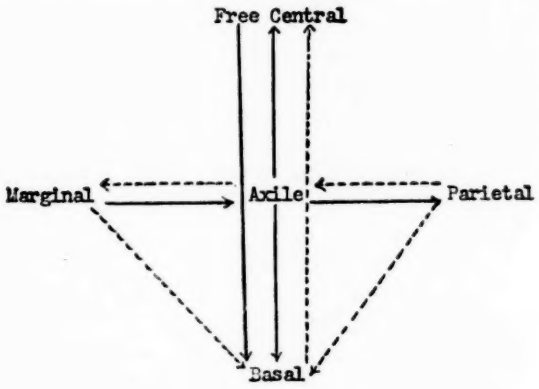


FIG. 14. Author's conception of the relationships between different types of placentation. Dotted arrows indicate possibilities of evolution, but these have yet to be proved.

Chenopodium and *Primula* as exhibiting the simplest type of placentation, the ovule being borne on direct continuation of the floral axis. Following this interpretation, Hagerup (1938, 1939) also considers parietal placentation as being obtained by a longitudinal splitting of the central placental axis into several branches which diverge and become appressed to the ovary wall along the line of fusion of carpellary margins.

From Fig. 14 it appears that "marginal" placentation (*sensu restricto*), as conceived here, is the simplest. This is the condition in monomerous gynaecea which are generally believed to be most primitive. The recent work of Bailey and his associates on some

[9] Lawrence (1937) has brought out an interesting correlation between the place of attachment of the style and that of the ovule in certain species of the Boraginaceae. With an apical style the ovule in each chamber is pendulous, whereas with a basal style the ovule is also basal.

of the more primitive Ranalian families appears to support such an inference in so far as it indicates clearly that the primitive carpel is a conduplicately folded structure and not a three-lobed leaf-like organ, as was earlier suggested (Sinnott and Bailey, 1914; Eames, 1931; Hunt, 1937; etc). If this is so, and there appears to be nothing to the contrary, it will furnish yet another argument for holding the marginal placentation as the simplest.

It is not so easy to decide whether axile or parietal placentation is more primitive, and the point perhaps is no less controversial than the nature of the placenta. Referring to this problem, Engler (1909) wrote: "When in a related group there is only parietal placentation, it is not necessary to assume that there is a progression from a many-celled ovary; for as soon as syncarpy arose either a many celled or one celled ovary might develop, according as the carpel margins were more or less bent inward".

Ordinarily, however, the condition is not so simple. Numerous attempts have been made to prove one type of placentation more primitive than the other. In Engler's system of classification parietal placentation is considered to be more advanced than axile. It was perhaps on this account that the Order Parietales was ranked so high in his system. Diels (1920), while giving a list of evolutionary trends in an angiosperm flower, states that evolution has progressed from "ovary cells, as many as the carpels, to less than these". He thus holds parietal placentation to be more advanced than axile. Joshi (1947) supported the same opinion. Detailed studies of different authors have revealed that parietal placentation in a number of families has been derived from axile placentation, e.g., Papaveraceae, Capparidaceae, Cruciferae, Moringaceae (Puri, 1945, 1950), Passifloraceae and Cucurbitaceae (Puri, 1947), Tiliaceae (Wiebel, 1945), certain Berberidaceae (Chapman, 1936), Orobanchaceae (Henslow, 1893), Apocynaceae (Woodson and Moore, 1938), Caprifoliaceae (Horne, 1914; Wilkinson, 1948*a*, *b*, 1949).

Some others believe that parietal placentation is more primitive than axile. This is based mainly on the oft repeated statement that it is associated with hypogyny and the polyandrous condition. Hutchinson (1929) wrote: "After syncarpy was attained, the parietal type of placentation generally preceded the axile basal or apical types, the axile being the final and most efficient condition". He restated the same opinion in 1948.

Parietal placentation in *Cornus* (Wilkinson, 1944) and in certain species of the Begoniaceae (Gauthier, 1950) and Gentianaceae (Lindsey, 1940) is considered antecedent to axile placentation. Lindsey believes that the unilocular condition of the ovary in the Gentianaceae is primitive and that from this, evolution has progressed in two directions. While in some species the placental zone has spread laterally from the commissures, involving much of the locule wall in bearing ovules, in others "placental outgrowths" from the carpellary edges have protruded in varying degrees toward the center of the locule. This tendency carried to its conclusion is believed by Lindsey to have produced bilocular ovaries in certain genera.

Gundersen (1939), who is a strong exponent of the view that parietal placentation is more primitive than axile, has discussed the problem at some length. He believes in ontogeny repeating phylogeny. He has observed a number of cases where, in bud condition, the ovary is unilocular with parietal placentation, and in mature flowers, multilocular with axile placentation. He thus asserts: "Among the numerous genera which have open center in the bud may be mentioned *Hibiscus, Tilia, Gordonia, Ruta, Ilex, Linum* and *Tropaeolum*. In all cases the change or suggestion of change is from parietal to axile placentation, never the reverse. In a number of cases, for example, *Shortia, Feijoa* and *Myrtus,* the upper part of the ovary has parietal placentation, the lower part axile. The reverse does not occur. Here, as with the petals, we must consider the upper part to represent the primitive condition".

With a view to marshal yet another argument for his opinion, Gundersen analyzes the literature concerning some families of the Parietales and comes to the conclusion that the high position which Engler accorded to this order is unjustifiable and unnatural. He evidently wants to convey the idea that neither parietal placentation nor the Parietales is so advanced as Engler thought.

Further he held that all placentae are fused together in axile placentation and free in parietal. He compares axile placentation to gamosepaly, gamopetaly and syncarpy, and parietal placentation to polysepaly, polypetaly, etc., and argues that what gamopetaly is to polypetaly, axile placentation is to parietal.

On closer examination of Gundersen's arguments for inferring parietal placentation as the most primitive, we can not help

feeling that they are unconvincing and readily yield to other interpretation [10] (see also Copeland, 1951). For instance, the observation that in many cases a multilocular ovary starts development as a unilocular structure can be easily explained without recourse to phylogeny. As has already been pointed out (Joshi, 1947), this may be due to the centripetal mode of growth so characteristic of the flower and flower parts. The usual acropetal succession is: sepals, petals, stamens and carpels. The same principle perhaps applies to the ovary whose peripheral part develops earlier than the central part. The delay in development of an organ, or part of an organ, is due to its peculiar method of growth and may not involve any phylogenetic considerations.

Again, his observation that in certain cases the ovary is multilocular below and unilocular above is not of much help in the solution of our problem. The present author has observed that in *Crataeva religiosa* and certain other capparids (Puri, 1950) the ovary is unilocular in the middle and "multilocular" in the upper and lower regions. More cases of this type can be cited from the well illustrated papers of Junell (1934), Wiger (1935), Arber (1938) and others; and the author will not be surprised if Dr. Gundersen himself finds a multilocular condition once again in the upper part of the ovary in some of the cases cited by him. Formation of a unilocular condition of the ovary in the middle region is, therefore, purely a spatial problem and seems to have nothing to do with phylogeny, as is believed by Gundersen.

Gundersen is perhaps right in criticizing Engler for ranking the order Parietales so high in his system (see Warming and Potter, 1932; Rendle, 1938; Wettstein, 1935). But it can not be argued that because the Parietales are not so highly evolved as Engler thought them to be, parietal placentation can not be more advanced than axile. The primitiveness of a group or order does not necessarily imply it is primitive in all respects. In the order Rhoeadales, for instance, which is commonly believed to be more primitive than the Parietales, the parietal placentation is held to be derived from axile (Puri, 1945, 1950), and there is no reason why it can not be so in the Parietales.

[10] In his recent book, Gundersen (1950) does not seem to feel so strongly about his view on parietal placentation. He now admits that in some cases the parietal condition may be derived.

Again, Gundersen's analogy of axile placentation and parietal placentation to gamopetaly and polypetaly, respectively, is not quite appropriate. To one who has faith in the so-called classical interpretation of the carpel—and Gundersen has not renounced his so far—the placentae are borne just on the inner side of carpellary margins; they are not independent structures. Accordingly in a multilocular ovary each placenta, formed by the fusion of two half placentae belonging to two margins of a carpel, is enclosed in a separate locule. It is necessarily walled off from other placentae belonging to other carpels. It is thus incorrect to say that in axile placentation all placentae are fused. We must, however, distinguish between two types of fusion. Each placenta as conceived here is formed by the fusions of two half placentae which may belong to the two margins of the same carpel, as in marginal or axile placentation, or to contiguous margins of two carpels, as in parietal placentation.

The present author is, therefore, inclined to believe that the evidence brought to prove that parietal placentation is more primitive than axile, is far from being conclusive. It may be that both of them appeared independently from marginal placentation (cf. Bailey and Swamy, 1951, Figs. 22–24). But it seems quite probable that in some cases at least parietal placentation has been derived from axile. The inverted placental strands, which are a peculiarity of axile placentation, have also been observed in certain cases of parietal placentation (Puri, 1945, 1947, 1950, 1952*a*). And this feature, if at all of some consequence, can not be accounted for in any other reasonable manner. In other cases no direct evidence is available, but some considerations seem to indicate that parietal placentation may in almost all cases be derived from axile placentation.

As pointed out by Joshi (1947), we get some evidence on this point from a comparison of gynaecea in those primitive groups of angiosperms (such as Ranales) in which both apocarpous and syncarpous types occur together. In this order, whenever a syncarpous gynaeceum is formed it is usually multilocular with axile placentation. It should also be noted that when the primitive condition of apocarpy passes into syncarpy and the carpels are only partly connate, the ovary is multilocular and the placentation is axile.

Yet another consideration is based on the assumption that fusion of parts belonging to the same unit structure is more primitive than fusion of parts belonging to two different unit structures. In "marginal" and axile placentation a single placenta is formed by fusion of two half placentae belonging to two margins of the same carpel. In parietal placentation, however, such fusion occurs between half placentae belonging to contiguous margins of different carpels; this latter, in the opinion of the author, is a more advanced condition. Gauthier (1950), on the other hand, wants us to believe that the union is "more intimate and (phylogenetically) earlier between the two adjacent carpels than between the two margins of the same carpel".

The evolutionary history of laminar placentation is not quite clear. Joshi (1947) writes: "From its restriction to certain primitive families of dicotyledons and monocotyledons, it appears to have developed at a very early stage in the evolution of the flowering plants, perhaps even before these had differentiated into dicotyledons and monocotyledons". Gundersen (1950) also believes that laminar placentation is primitive. That it can also be derived from ordinary placentation, in which the ovules are confined to carpellary margins, is indicated in the Gentianaceae. In this family the unilocular condition is believed to be primitive and evolution is considered to have progressed along two different lines (Lindsey, 1940). While in some species "placental outgrowths" from the carpellary edges have protruded in varying degrees toward the center of the locule, in others the placental zone has spread laterally from the commissures covering, as it were, much of the locule wall. If this latter tendency is carried to its conclusion it may produce laminar placentation.

PLACENTATION AS A CHARACTER IN CLASSIFICATION

Before discussing the role of placentation as a character in taxonomy it is worthwhile to bear in mind the warning given by Rensch (1934): "Even if the taxonomic value of a character has been 'proved' in a hundred cases it still may fail in the hundred and first. The golden rule therefore is: there is no golden rule".

The taxonomic significance of placentation has long been recognized. It was perhaps Lindley who, by creating the order Parietales in 1830, accorded it the greatest recognition as an important

taxonomic character. This is indeed a living tribute to placentation from an outstanding personality.

Referring to the taxonomic significance of placentation, Gundersen (1939, p. 294) wrote: " In zoology, the coming of placental mammals makes a definite step in evolution, namely increasing care of the next generation. In botany the term ovulary has been proposed. Whatever the name, to assign to placentation a more important place in classification of the higher plants calls attention to a significant analogy between plant and animal evolution ".

Troll (1928) has attached special significance to placentation in " Gestalt " morphology. He distinguishes sharply between a " paracarpous " gynaeceum with parietal placentation and a " syncarpous " gynaeceum with axile placentation. He considers that the two forms are quite distinct, the fertile part of the " paracarpous " ovary being equivalent to the stylar segment alone of the " syncarpous ". Arber (1942, p. 47), who does not accept Troll's rigid classification of the gynaeceum into paracarpy and syncarpy, writes: " No one who is accustomed to looking at microtome series through the ovary can fail to be aware of the impossibility of drawing a rigid distinction between parietal and axile placentation ". Winkler (1941) has expressed a similar opinion. The present author (Puri, 1950) has observed cases where the ovary is multilocular in the lower and upper regions but unilocular in the middle. Such cases can not be easily explained if we accept Troll's interpretation of syncarpy and paracarpy.

It seems true, therefore, that such a rigid distinction as is claimed by Troll can not be maintained. Nevertheless, it can not be denied that studies in placentation and gynaeceum structure have been of considerable help in determining relationships and phylogeny. The following considerations will bear out such an inference.

On the basis of Eber's (1934) detailed studies on Helobiales, Just (Wilson and Just, 1939) concludes that " It is more probable that the Helobiae should be derived from the Nymphaeaceae (and Ceratophyllaceae) among the Polycarpicae (Ranales) than from the Ranunculaceae and their ancestors ". He further infers that " The structure of the carpels and placentation in *Ceratophyllum* conform with those of the Nymphaeaceae and resemble remarkably those of the Helobiae, especially the Potamogetonaceae. This

knowledge aids in the phylogenetic derivation of the Monocotyledons ".

Recent investigations on placentation in the Passifloraceae and Cucurbitaceae have revealed an interesting feature (Puri, 1947). In both cases the placentae are found to possess inverted strands which normally characterize the axile placentae. As a result of this feature the two families, whose affinities have already been recognized (Rendle, 1938; Harms, 1925; Hutchinson, 1926; Reuter, 1926), stand closer together than ever before [11]. Further, the same condition has also been reported in certain Rhoeadalean families (Puri, 1941, 1945, 1950). This confirms the inclusion of the Moringaceae in the Rhoeadales and also strengthens the suggestion of a link between the Moringaceae in the Rhoeadales and the Passifloraceae in the Parietales (see Harms, 1925; Wettstein, 1935). It is significant to note that in the first delimitation of Parietales by Lindley (1830) all these families except the Cucurbitaceae were included in the order Parietales.

Again, placentation has been made the basis for the suggestion that the Caryophyllaceae and the Primulaceae are closely related (Hutchinson, 1926; Douglas, 1936; Dickson, 1936) and that the latter have been derived from the former. The implication of such a suggestion is significant in so far as it minimizes the rigidness of the distinction between Polypetalae and Gamopetalae which were once considered as fundamentally distinct groups.

Placentation has long been regarded as an important character in the classification of the Ericaceae (see Palser, 1951) and the large ticklish genus *Begonia*. Irmscher (1925) has based his key for different sections of this genus on the placentae being " simple " or " bilamellate ". Gauthier (1950), while recognizing in a general way the usefulness of this character, cautions us, for in some species or groups of species it may not be so reliable as in others.

During recent years Lam (1948*a*, *b*, 1950) has been perhaps the strongest exponent of placentation as a character in taxonomy. Basing his conclusion on the place of attachment of sporangia

[11] Work is in progress in this Laboratory on the Caricaceae, a family often placed very near the Passifloraceae and Cucurbitaceae. So far only *Carica papaya* has been studied (Shanti Devi, 1951). It is significant to note that the placental vascular supply in this small family is not very different from that in the Cucurbitaceae.

(both micro and mega), he has proposed a new system of classifying Cormophyta into Stachyosporae and Phyllosporae. According to him stachyosporous plants are those in which true sporophylls are lacking and in which the sporangia are essentially terminal on fertile telomes. In phyllosporous plants, on the other hand, "the sporangia are essentially borne on many-telomed sterile fronds, which therefore deserve the denotion of sporophylls" (Lam, 1948*a*). In a more recent paper he asserts (Lam, 1950, p. 527): "The most convincing and the widest spread evidence towards stachyo- and phyllospory, however, is offered by the placentation of the ovules: in the Stachyosporae it is primarily basal (central) on the axis and the ovules are often orthotropous; in the Phyllosporae it is primarily marginal on sporophylls, the ovules often being anatropous".

Among stachyosporous plants are included the Bryopsida, the Psilopsida, the Lycopsida, the Sphenopsida, female Bennettitales, the Coniferopsida (except those displaying secondary phyllospory in the cladosporophylls and except male conifers which are mainly phyllosporous), the protangiosperms[12] and some angiosperms, while phyllosporous plants are the Pteropsida (except the Caytoniales), the Cycadopsida (except the female Bennettiales), male conifers (except *Taxus*) and angiosperms. Angiosperms are believed to be predominantly phyllosporous, but stachyospory occurs also in many families of the Monochlamydeae, e.g., the Salicales, Myricales, Juglandales, Urticales, Centrospermae and possibly also the Euphorbiaceae, some monocotyledons (Pandanaceae) and perhaps even in some Sympetalae (Plumbaginales, Primulales). Phyllosporous and stachyosporous angiosperms have been shown to have been quite distinct from the very beginning (Cretaceous). As to the distribution of phyllospory and Stachyospory in the male and female sexes, Lam (1948*b*) writes: "There seems to be some preference for the development of phyllospory in the male sex (Bennettitales, Coniferae, Cordaitales?). Whether this applies also to angiosperms in still unknown".

As a detailed critical analysis of this "New Morphology" and the new system of classification has just been published (Eames, 1951), it does not seem necessary to go into details here. It may be mentioned, however, that such natural groups as the Caryophyllaceae have been divided into two major divisions which allegedly

[12] Lam's conception of protangiosperms is different from that of Engler.

have been distinct since the Devonian [13]. The classification appears to be ill conceived, at least so far as the angiosperms are concerned. Maybe, as Lam (1948*a*, p. 148) points out, our mind has " too much inertia to readily abandon the names and concepts with which we have grown up scientifically ". But it is equally important that the pendulum does not swing too much to the other side, for then it will result in chaotic conditions which beget nothing but confusion.

MORPHOLOGY OF PLACENTAE

The morphological nature of placentae in angiosperms has long remained controversial. While the majority of workers agree that it is carpellary in all cases, others believe that it is receptacular in some or in all angiosperms. The different views held from time to time seem to fall under the following categories:

a) Placentae in all angiosperms are axial structures.

b) Placentae are not of the same nature in all cases.

c) Placentae in all angiosperms are carpellary structures.

The axial nature of the placentae in angiosperms was formally suggested perhaps for the first time by St. Hilaire (1816, 1847). He stated that the floral axis, after producing the carpellary leaves, continues up and bears ovules which may be borne on the central column or on its branches, as in parietal placentation. This view was more emphatically put forward by Schleiden (1849) and subsequently by Payer (1857) who also believed that the margins of the carpellary leaf derive their power of bearing ovules from being overlain with outgrowths of the branched floral axis.

Subsequent authors, however, did not pay heed to this view till recently when McLean Thompson (1934, and others) Hagerup (1938, 1939), Gregoire (1935, 1938), Thomas (1931, and others) and Plantefol (1949) tried to revive it in some form but with little success. While all these authors believe that the placenta in angiosperms is an axial structure, they differ in their concept of the carpel. Thompson denies the existence of carpels altogether, while Hagerup (1938, 1939) believes that they do exist but merely form an involucre of coalescing and barren leaves around the floral axis

[13] In his recent chart Lam (1950, Fig. 1) shows angiosperms as a single group, partly stachyosporous and partly phyllosporous, in contrast to the condition shown in his previous chart (Lam, 1948*a*, Fig. 19) where stachyospory and phyllospory are indicated to have arisen quite independently from different sources.

bearing ovules. In ovaries with parietal placentation the ovuliferous floral axis is believed to have split into several distinct parts which become attached to the ovary wall at the junction of carpellary margins (cf. St. Hilaire, 1847). Hagerup interprets the ovules as monosporangiate megasporophylls.

This concept of the axial nature of placentae was formulated largely on account of the supposed axial nature of the ovule. St. Hilaire, Schleiden, Payer and to some extent Braun regarded the ovule as a modified bud which, as a rule, is borne on axial parts. The extensive researches of Čelakovsky (1875, 1876, and others), Warming (1878), Strasburger (1879, and others) and many others (for details see Worsdell, 1904) have, however, shown that the bud nature of the ovule is no longer tenable. Rather it is to be regarded as a new structure corresponding to the megasporangium of Pteridophytes. This takes away, as it were, much of the basis for the axial nature of placentae.

About the middle of the last century many authors held the view that a placenta is not of the same morphological nature in all cases. Though most of them believed that in the great majority of cases it is carpellary, it was conceded that in some cases it is of different origin. This is clear from the early writings of Treviranus (1838), Brongniart (1844), Balfour (1854) and others. Huisgen elaborated this idea further in his thesis published in 1873. He distinguished three types of placentae. In the Primulaceae, Solanceae, Lobeliaceae, Ericaceae, Malvaceae and Hypericaceae he regarded the placenta as a prolongation of the axis, while in the Violaceae, Leguminosae and in the monocotyledons it was considered to be carpellary, and in the Cruciferae and Resedaceae as an independent organ, probably of the nature of a phyllome, a view which Barcianu (1875) is said to have applied later to the condition in the Onagraceae (see Sachs, 1882).

Workers in the present century, however, have attached little significance to such treatment. Nevertheless some authors still think that the placenta is axial in some cases, as in the Primulaceae, Solanaceae, Juglandaceae, Piperaceae and *Najas*. A detailed consideration of these types will follow a little later.

Vuillemin (1926) has put forward a somewhat different view. According to him, a carpel is composed of two heterogeneous members, a phyllome and a frondome, associated in development. He bases his theory on certain points in floral morphology and on

some abnormalities, including a case said to have been described by Baillon (1880) where a virescent flower of *Delphinium consolida* had its placenta free and inside the open carpel.

The third view, that a placenta is a carpellary structure, is contained in the early writings of Robert Brown (1816, 1822, 1840, etc). He considered in detail all the principal modifications of a compound ovary with different types of placentation and found no fundamental difference between parietal and free central placentation which was believed to have resulted through complete absorption of septa (Brown, 1840). Later van Tieghem (1871), Čelakovsky (1875; and others), Lister (1884), Henslow (1890) and many others supported this view. In the present century this is being upheld by most workers, including Horne (1914), Eames (1931), Troll (1939), Douglas (1944), Wilson and Just (1939), Joshi (1947) and Puri (1951).

It may be worthwhile to examine critically the arguments that have been advanced from time to time against this view. As far as could be ascertained there are three conditions on which rejection of the carpellary nature of the placentae can be based:

a) The independence of the vascular systems supplying the ovary wall and the placentae.

b) The enormous disproportion between the size of the placentae and that of the carpellary valves in various plants, e.g., the Solanaceae and Gentianaceae.

c) The isolation of the placentae in the Primulaceae, Juglandaceae, Piperaceae and other families.

Attention has already been drawn to the fact that in the majority of cases the ventral system of vascular bundles of a carpel are quite distinct from its dorsal system. One, so to say, does not interfere in the domain of the other. At first sight this may appear to support the view that placentae are distinct structures, quite independent of carpels. Actually, however, this may not be so, for each placenta is a double structure and receives double vascular supply corresponding to two carpellary margins. If it were entirely an independent [14] structure, its vascular supply need not have been double. Further, in some of the primitive families this distinctiveness of the two systems is not maintained; for instance, in the Nymphaeaceae (Saunders, 1936) and certain other

[14] See also discussion ahead.

Ranales (Bailey and Nast, 1943; Nast and Bailey, 1945) the dorsal bundles are also known to contribute traces for the ovule. It appears, therefore, that this distinctiveness is consequent upon a division of labor which is necessitated by the ovule-bearing function of the carpel.

In certain families, particularly the Solanaceae, Ericaceae, Gentianaceae and some other Bicarpellatae, the placentae become very massive. Their prominent size gives them a degree of distinctiveness. It was perhaps this feature which led some workers to interpret the placentae in the Solanaceae as of axial origin (Vidal, 1900; Warner, 1933; Urquhart, 1943). Satina and Blakeslee (1934) have reached the same conclusion, though from a different direction. Recently, on the basis of a detailed anatomical study of the placental condition in the Solanaceae, Murray (1945) has concluded that the ovule-bearing portions of the placentae are carpellary and that the central parenchymatous part of the ovary is receptacular to a greater or less extent. There is little doubt that also in the other Bicarpellatae the condition is more or less the same.

In the Cucurbitaceae, too, the placentae are very massive and reflexed outward. At the base of the ovary in many species there is a central core of vascular tissue having xylem in the center completely surrounded by phloem. In the ovule-bearing region this central core breaks up into three inversely oriented placental strands [15]. It is near this point that the axis ends and the carpels begin, at least so far as the center of the ovary is concerned. The placentae have these inverted bundles and therefore are carpellary (Puri, 1952*b*). In the light of these observations the earlier view that the placentae in the Cucurbitaceae are axial (Kirkwood, 1905) is wholly untenable.

Isolation of the placentae from the ovary wall in certain families is, perhaps, the strongest argument in the hands of those who do not believe in the carpellary origin of placentae. Much of the controversy has centered around this point. It is perhaps a part of the ever insoluble (?) problem: "Where does the axis end and the leaf begin?" Dealing with the problem in the Primulaceae, Goebel (1905) wrote: "In the free central placenta we should

[15] One of the author's pupils, S. P. Rastogi (1951), has observed a similar change in the orientation of the bundles in the placental region of certain species of the Myrtaceae.

distinguish neither appendicular nor axial parts". This is perhaps the safest course to adopt. But a modern scientist is perhaps more reckless in the sense that he cares more for finding unity behind diversity than for safety! During recent years much more information has accumulated than was available to the authors of the last century. It will, therefore, be worthwhile to review briefly the literature concerning some of those families in which the placentae are more or less completely separated from the ovary wall.

In any discussion of the nature of placentae, the Primulaceae have always figured prominently. The earlier literature on the subject has been admirably reviewed by Douglas (1936). A few remarks, therefore, will serve the purpose here. Referring to the subject, Goebel (1905, p. 556) wrote: "'Orthodox morphology' considers the central placenta as formed out of the axis on which run up the basal portions—the soles—of the carpels", and declared the placenta to be the continuation of the flower axis alone. The anatomical school, on the other hand, regards the placenta as formed from the carpellary soles alone, because it is pierced by a system of conducting bundles, which have their vascular portion turned outwards and are connected with the conducting bundle-system of the carpels. This condition, however, is by no means general; where the placenta is weak, the supply of vascular bundles is simplified. In *Primula farinosa*, for example, there is a simple concentric strand in the middle of the placenta, and the same is true of *Androsace villosa* and others (see Vidal, 1900). From this we learn that the anatomical structure gets its direction after formation of the placenta and is not inverted; in other words, the relationships of the vascular bundles are determined by the claims of physiology, not by those of morphological behaviour".

This is not fair treatment to the anatomical method from one so influential and authoritative. It is apparent that in those cases where the placental bundles are inverted they give clear indication of the existence of carpellary margins in the placental column. It is true that in some cases (e.g., van Tieghem, 1871) too much has been explained on the basis of anatomical structure. For instance, the occurrence of a cylinder of inverted placental strands can not possibly negate the existence of some amount of receptacular tissue in the pith of the placental column, unless of course the condition is similar to that described above for the Cucurbitaceae (cf. Eckardt, 1939). Here, of course, the person who employs the method is to

blamé and not the method itself. Again, in reduced cases the vascular tissue may also be reduced and modified according to the needs. This can be a sound reason for discarding the so-called doctrine of conservatism of vascular tissue (see Puri, 1951), but surely it does not call for a general condemnation of the anatomical method.

The modern view, therefore, about the nature of the placental column in the Primulaceae seems to be that it is formed by carpellary margins and that through this extends the floral axis of a greater or less extent. Such a view is supported by studies in teratology (Heinricher, 1932, 1933), anatomy (Dickson, 1936) and ontogeny (Schaeppi, 1937).

The condition in *Typha, Najas* and Piperaceae is of special interest in this connection. In these cases the very simple female flower consists of almost nothing but a small lateral shoot bearing an ovary with a central ovule which appears as a direct continuation of the floral axis. There is therefore no distinct placenta. Hanstein and Schmitz (1870), Magnus (1869, 1894) and Payer (1857) held not only that the ovule as a whole is axial but also that the nucellus itself is a terminal srtucture (see Sachs, 1882).

Sachs (1882, p. 564) mentions a personal letter from Schenk in which he (Schenk) " distinctly denies the axial nature of the ovule in *Typha;* he states that it is lateral, that it appears as a small protuberace on the wall of the ovary, a position which it retains until maturity ". Similarly Eber (1934), who has made a detailed study of placentation in the Helobiales, has reached the conclusion that the condition in *Najas* is derived from that in the rest of the Potamogetonaceae which she describes as " terminal-median ".

Recently a colleague of the author, Mr. Y. S. Murty, has started a reinvestigation of some species of the Piperaceae, especially with the idea of tackling the problem of placentation in this family and certain allied ones. While Murty (1952) has found apparently terminal ovules in some species, he has obtained fairly reliable anatomical evidence in certain others, for interpreting the ovules as distinctly lateral. It appears certain, therefore, that the apparently basal ovule in the Piperaceae has been derived from a lateral position, much in the same fashion as the ovule in *Boehmeria* (Bechtel, 1921). It may be remembered that Baillon (1874) also spoke of the ovules in the Piperaceae as being " sub-basal ".

The situation in the Polygonaceae has been recently reviewed

and studied in detail by Laubengayer (1937). He supports the view held earlier by Cramer (1869), Henslow (1893) and Čelakovsky (1899) that the ovule is actually carpellary and that its basal position is derived. He further concludes that the base of the cavity is not the base of the ovary which has become solid for one-third its height and that the ovule which appears to occupy a basal position is really terminal to the placental axis. The " funiculus " of the ovule, therefore, according to Laubengayer, is not the simple stalk of the ovule, as in most angiosperms; instead it represents a free central placenta which is greatly reduced. Joshi (1938), while accepting the derived position of the ovule, does not agree with Laubengayer's interpretation of the " funiculus " which he considers as a real funiculus and not a placenta.

The nature of the ovule in the Juglandaceae, particularly in *Juglans regia,* has long remained controversial. Van Tieghem (1869*a*), on the basis of his anatomical studies, came to the conclusion that the single ovule, though apparently terminal and orthotropous, is really an outgrowth from the carpels and is anatropous. This view has been wholly (Benson and Welsford, 1909) or partly (Manning, 1938, 1940) supported in subsequent years. There are others who believe in the axial nature of the ovule (Nicoloff, 1903; Shuhart, 1932; Langdon, 1939). They base their conclusion on the observation that in very young stages the ovary is unilocular, having a central column which bears the ovule, and that it is only later that the carpellary septa arise and divide the ovary into two chambers. Nast (1935), who does not commit herself to either of these views, also notes this feature in her young material and writes: " If, however, longitudinal sections of older flowers cut through the septum are examined there is no central column but the ovule is borne directly upon the united carpel edges ".

Anatomical structure, however, appears to support the appendicular view. Even Langdon's observations can be used to support this view, for she describes and illustrates the placental bundles in *Juglans mandchurica* as undergoing a down-turning before entering the placental column, suggesting thereby that the ovule has descended during phylogeny from a higher position.

The placentation in the Santalaceae, Loranthaceae and allied families has also attracted some attention. Owing perhaps to the parasitic mode of life, these families are all reduced to a greater or less extent, and in certain Loranthaceae and Balanophoraceae

(Fagerlind, 1945, 1948) the reduction has proceeded to such an extent that there develops nothing that may be called an ovule or even a placenta. In *Balanophora,* for instance, the embyo sac mother cell differentiates in the middle of some carpellary tissue that does not seem to develop into an ovule. Fagerlind (1945) shows schematically how this peculiar structural condition in *Balanophora* can be obtained through gradual reduction from the Santalaceae.

The nature of the central column bearing ovules in the Santalaceae has been variously interpreted. Anatomical and ontogenetic studies support the interpretation that it is either wholly (van Tieghem, 1869*b;* Smith and Smith, 1942*a, b*) or partly (Schaeppi und Steindl, 1937; Schaeppi, 1942) carpellary. Smith and Smith (1942*b*) have based their conclusion on the observation that in many cases they have seen what they call the residual tissue of the floral axis as being directed downward. If this is so, the floral axis is inverted and consequently it can not participate in the formation of the placental column which must necessarily be wholly carpellary. The present author, however, finds it difficult to imagine how the so-called " invagination " of the floral axis can invert the floral apex. The point at issue is not of much consequence to us here; what is significant from our point of view is that at least the peripheral part of the placental column is carpellary and that the ovules originate from this region. The casual reports that the placental column in the Santalaceae is " axial " (Johnson, 1889; Rao, 1942) can not be taken seriously.

In the Loranthaceae also, wherever the placental column exists, it has been interpreted as of " mixed nature ", the peripheral region being carpellary, the central core axial (Schaeppi und Steindl, 1942, 1945).

There is yet another point to be considered before we close. In some recent writings the placenta has been treated as a distinct structure arising probably as an outgrowth from carpellary margins and distinguished more or less clearly from them. Heinig (1951), for instance, considers that in *Phaleria* (Thymelaeaceae) the two parietal placentae extend inward, carrying the ovules in the center and dividing the ovarian cavity falsely into two loculi. Evidence for such an interpretation is found in the occurrence of the carpellary ventrals in the ovary wall instead of in the middle of the septum which should have been the case if the ovary were

truly bilocular with axile placentation. She writes: " Whereas the septum in the Aquilarioideae is clearly made up of the involuted margins of adjacent carpels, the parietal position of the commissural carpellary bundles in *Phaleria* necessitates the interpretation of the septum in this genus as being formed by adaxial extensions of opposite placentae ".

It is quite likely that such a condition is more common than is known at present (see Horne, 1914; Wilkinson, 1944; and cf. figs. in Junell, 1934; Leinfellner, 1951; Lindsey, 1940; Wiger, 1935). The placentae here are more or less distinctive structures though not necessarily independent organs. They are perhaps best described as enlargements of certain areas along the margins of carpels. In Cucurbitaceae, however, the condition is not what is implied by many taxonomists and text-book writers who describe the ovary as " falsely " or " spuriously " trilocular. Here the inverted bundles occurring in the inner edges of the placentae are interpreted as carpellary ventrals which indubitably mark the limits of carpellary margins (Puri, 1952*b*).

Fagerlind, who has applied the telomic concept to the angiosperm ovule, writes about placenta as follows: " Die Placenten werden als Achselderivate der Fruchtblätter angesehen, die mit ihren Stützblättern und mit der Spitze der Blütenachse mehr oder weniger stark kongenital verwachsen sind " (Fagerlind, 1946, p. 54).

In conclusion it may be stated that, although in all cases the placentae can satisfactorily be explained as carpellary structures, we need not be too dogmatic about this view. The days are long past when the leaf was considered a fundamental part of the plant body. Now it is almost a descriptive term, serving convenience more than anything else. This being so, the appendicular versus axial controversy loses much of its original significance and attraction. Mrs. Arber, whose contribution to angiosperm morphology is perhaps the most significant of all, has recently restated the case for the partial-shoot theory of leaf and carpel. In the light of this theory she sums up her views on the controversy between carpellary and axial placentae in these words (Arber, 1950, p. 131): " This difference of opinion would lose its significance if we suppose that the fertile lobes, by natural fusion, may together rise to the radiality of a whole-shoot, and thus form a structure comparable to an axillary bud ".

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LITERATURE CITED

ARBER, A. 1913. On the structure of the androecium in *Parnassia*. Ann. Bot. **27:** 491–510.
————. 1925. Monocotyledons.
————. 1929. Studies in the Gramineae. VIII. On the organization of the flower in the bamboo. Ann. Bot. **43:** 765–781.
————. 1934. The Gramineae—A study of cereal, bamboo and grass.
————. 1938. Studies in flower structure. IV. On the gynaeceum of *Papaver* and related genera. Ann. Bot. (N.S.) **2:** 649–663.
————. 1942. Studies in floral structure. VII. On the gynaeceum of *Reseda*, with a consideration of paracarpy. Ann Bot. (N.S.) **6:** 43–48.
————. 1950. The natural philosophy of plant form.
BAILEY, I. W. and NAST, C. G. 1943. The comparative morphology of the Winteraceae. II. Carpels. Jour. Arn. Arb. **24:** 472–481.
———— and ————. 1945. The comparative morphology of the Winteraceae. VII. Summary and conclusions. Jour. Arn. Arb. **26:** 37–47.
————, ———— and SMITH, A. C. 1943. The family Himantandraceae. Jour. Arn. Arb. **24:** 190–206.
———— and SWAMY, B. G. L. 1949. The morphology and relationships of *Austrobaileya*. Jour. Arn. Arb. **30:** 211–226.
———— and ————. 1951. The conduplicate carpel of dicotyledons and its initial trends of specialization. Am. Jour. Bot. **38:** 373–379.
BAILLON, H. 1874. The natural history of plants. Vol. III. [Engl. Trans. by Hartog].
BALFOUR, J. H. 1854. Class book of botany.
BANCROFT, H. 1935. A review of researches concerning floral morphology. Bot. Rev. **1:** 77–99.
BAUM, HERMINE. 1948. Vergleichende, morphologische, anatomische und entwicklungsgeschichtliche Untersuchungen über die *Astragalus*-Frucht. Ann. Naturalhist. Mus., Wien **56:** 246–261.
BECHTEL, A. 1921. The floral anatomy of the Urticales. Amer. Jour. Bot. **8:** 386–410.

BELZUNG, E. 1900. Anatomie et physiologie végétales.
BENSON, M. and WELSFORD, E. L. 1909. The morphology of the ovule and female flower of *Juglans regia* and a few allied genera. Ann. Bot. **23:** 623–633.
BENTHAM, G. and HOOKER, J. D. 1912. Handbook of the British flora.
BLASER, H. W. 1941*a*. Studies in the morphology of the Cyperaceae. I. Morphology of the flowers. A Scirpoid genera. Am. Jour. Bot. **28:** 542–551.
————. 1941*b*. Studies in the morphology of the Cyperaceae. I. Morphology of the flowers. B. Rynchosporoid genera. Am. Jour. Bot. **28:** 832–838.
BONNIER, G. et LECLERC DU SABLON. 1919. Cours de botanique. Phanerogames.
BRAUN, A. 1874. Bemerkungen über Plazentenbildung. Verh. Bot. Ver. Prov. Brandenburg, VIII. Sitzungsber, vol 30 Jan., pp. 45–50.
BRONGNIART, A. 1844. Examen de quelques cas de monstruosités végétales propers à éclairer la structure du pistil et l'origine des ovules. Arch. Mus. Hist. Nat. **4:** 43. [Quoted from Worsdell, 1904].
BROWN, R. 1816. Some observations on the natural family of plants called Compositae. Trans. Linn. Soc. London **12:** 76–142.
————. 1822. An account of a new genus of plants, named *Rafflesia*. Trans. Linn. Soc. London **13:** 201–234.
————. 1840. On the relative position of the divisions of stigma and parietal placentae in the compound ovarium of plants. Misc. Bot. Works of Robert Brown.. Vol. 1: 555–563. 1866.
BUXBAUM, F. 1951. Grundlagen und Methoden einer Erneuerung der Systematik der höheren Pflanzen.
CAMPBELL, E. 1930. General elementary botany.
ČELAKOVSKY, L. J. 1875. Ueber die morphologische Bedeutung der samenknospen Flora **57:** 225–238.
————. 1876. Vergleichende Darstellung der Plazenten in den Fruchtknoten der Phanerogamen. Abhandl. König. Böhm. Ges. Wiss. Prag **8**(6).
————. 1899. Ueber achtzahlige Cyklen pentamer veranlegter Blüthen. Jahrb. Wiss. Bot. **33:** 368–415.
CHAPMAN, M. 1936. Carpel anatomy of the Berberidaceae. Am. Jour. Bot. **23:** 340–348.
CHAUVEAUD, B. G. 1892. Sur l'insertion dorsale des ovules chez les Angiosperms. Compt. Rend. Acad. Sci. [Paris] **113:** 141. [Quoted from Goebel, 1933].
CHUTE, H. M. 1930. The morphology and anatomy of the achene. Am. Jour. Bot. **17:** 703–722.
CRAMER, K. 1869. Bildungsabweichungen bei einigen wichtigeren Pflanzenfamilien und die morphologische Bedeutung des Pflanzencies.
COPELAND, H. F. 1951. "Families of dicotyledons by A. Gundersen"—A review. Madroño **11:** 149–151.
DEVI, S. 1951. Vascular anatomy of the flower of *Carica pápaya*. [Unpub. thesis, Agra Univ.]
DICKSON, JEAN. 1935. Studies in floral anatomy. II. The floral anatomy of *Glaucium flavum* with reference to other members of the Papaveraceae. Jour. Linn. Soc., Bot. **50:** 175–224.
————. 1936. Studies in floral anatomy. II. An interpretation of the gynaeceum in the Primulaceae. Am. Jour. Bot. **23:** 385–393.
DIELS, L. 1920. Die Methoden der Phytogeographie und der Systematik der Pflanzen.
DOUGLAS, GERTRUDE E. 1936. Studies in the vescular anatomy of the Primulaceae. Am. Jour. Bot. **23:** 199–212.
————. 1944. The inferior ovary. Bot. Rev. **10:** 125–186.
DUTTA, A. C. 1933. A class-book of botany.

EAMES, A. J. 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Am. Jour. Bot. **18:** 147–188.
————. 1951. Again: "The New Morphology". New Phyt. **50:** 17–35.
———— and MACDANIELS, L. H. 1947. An introduction to plant anatomy. Sec. Ed.
———— and WILSON, C. L. 1928. Carpel morphology in the Cruciferae. Am. Jour. Bot. **15:** 251–270.
EBER, ERNA. 1934. Karpelbau und Plazentationsverhältnisse in der Reihe der Helobiae. Flora **127:** 273–330.
ECKARDT, THEO. 1937. Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung des pseudomonomeren Gynoeciums. Nova Acta Leopoldina (N.F.) **5:** 1–112.
————. 1938. Das pseudomonomere Gynoecium. Chron. Bot. **4:** 206–208.
————. 1939. Vergleichende Morphologie des Gynaeceums und der Karpelle. Chron. Bot. **5:** 153.
EGGERS, O. 1935. Über die morphologische Bedeutung des Leitbündelverlaufes in der Blüthen der Rhoeadalen und über das Diagramm der Cruciferen und Capparidaceen. Planta **24:** 14–58.
ENGLER, A. 1909. Syllabus der pflanzenfamilien.
FAGERLIND, F. 1945*a*. Bau des Gynöceums der Samenanlage und des Embryosackes bei einigen Reprasentanten der Familie Icacinaceae. Svenska Bot. Tidskr. **39:** 246–264.
————. 1945*b*. Blüte und Blütenstand der Gattung *Balanophora*. Bot. Not. **1945:** 330–350.
————. 1946. Strobilus und Blüte von *Gnetum* und die Möglichkeit aus ihrer Structur den Blütenbau der Angiospermen zu deuten. Arkiv Bot. **33A:** 1–57.
————. 1948. Beiträge zur Kenntnis der Gynaceummorphologie und Phylogenie der Santalales-Families. Svenska Bot. Tidskr. **42:** 195-229.
FULLER, H. J. and TIPPO, O. 1949. College botany.
GAUTHER, R. 1950. The nature of the inferior ovary in the genus *Begonia*. Univ. Montreal, Inst. Bot. Contr. 66, 1–93.
GERBER, C. 1900. Recherches sur le nombre des feuilles carpellaires qui entrent dans la constitution du gynécée des Crucifères. Bull. Sci. France et Belique **33:** 493–521.
GOEBEL, K. 1905. Organography of plants. [Eng. trans. by Balfour].
————. 1933. Organographie der Pflanzen. III. Tiel. Samenpflanzen.
GRAY, A. 1879. Structural botany.
GREEN, J. R. 1904. A manual of botany. Vol. 1. Morphology and anatomy.
GREGOIRE, V. 1935. Les anomalies florales des *Primula* et la valeur du placenta central. Ann. Soc. Sci. Bruxelles **60:** 297–301.
————. 1938. La morphogénèse et l'anatomie morphologique de l'appareil floral. I. Le carpelle. La Cellule **47:** 287–452.
GUNDERSEN, A. 1939. Flower buds and phylogeny of the dicotyledons. Bull. Torrey Bot. Club **66:** 287–295.
————. 1950. Families of dicotyledons.
HAGERUP, O. 1938. On the origin of some angiosperms through Gnetales and the Coniferae. III. The gynaeceum of *Salix cinerea*. Kung. Danska Vid. Selsk. Biol. Med. **14:** 1–34.
————. 1939. On the origin of some angiosperms through the Gnetales and the Coniferales. IV. The gynaeceum of Personatae. Kung. Danska Vid. Selsk. Biol. Med. **15:** 1–39.
HANSTEIN und SCHMITZ. 1870. Ueber die Entwicklungsgeschichte der Blüthen einiger Piperaceen. Bot. Zeit. **28:** 37-40.
HANNIG, E. 1901. Untersuchungen über die Scheidewände der Cruciferen. Früchte. Bot. Zeit. **59:** 207–245.

HARMS, H. 1925. Passifloraceae. *In* Engler und Prantl, 'Die natürlichen Pflanzenfamilien'. Vol. 21.
HARRIS, W. T. and STURGES, A. F. 1919. Webster's New International Dictionary of English Language.
HEINIG, KATHERINE H. 1951. Studies in the floral morphology of the Thymelaeaceae. Am. Jour. Bot. **38:** 113-130.
HEINRICHER, E. 1932. Beiträge zur Morphologie der Primulaceen-blüten. Ber. Deut. Bot. Ges. **50:** 4-7.
————. 1933. Zur Frage nach dem Bau der Primulaceen Plazenta. Ber. Deut. Bot. Ges. **51:** 304–316.
HENSLOW, G. 1890. On the vascular systems of floral organs, and their importance in the interpretation of the morphology of flowers. Jour. Linn. Soc., Bot. **28:** 151–197.
HOOKER, J. D. and THOMPSON, T. 1858. Praecursores and Floram Indicam. Jour. Linn. Soc., Bot. **2:** 54.
HORNE, A. S. 1914. A contribution to the study of the evolution of the flower, with special reference to the Hamamelidaceae, Caprifoliaceae, and Cornaceae. Trans. Linn. Soc., London II. **8:** 239–309.
HUISGEN, F. 1873. Untersuchungen über die Entwicklung der Placenten. Diss. Bonn.
HUNT, K. W. 1937. A study of the style and stigma, with reference to the nature of the carpel. Am. Jour. Bot. **24:** 288–295.
HUTCHINSON, J. 1926. The families of the flowering plants. Vol. I. Dicotyledons.
————. 1929. The phylogeny of flowering plants. Proc. Int. Cong. Plant Sci., Ithaca. (1926) Vol. 1: 413–442.
————. 1948. British flowering plants.
IRMSCHER, E. 1925. Begoniaceae. *In* Engler und Prantl, Die natürlichen Pflanzenfamilien. Vol. 21.
JOHNSON, T. 1889. The nursing of embryos and some other points in *Myzodendron punctulatum* Banks et Sol. Ann. Bot. **3:** 179–206.
JONES, S. C. 1950. Introduction to floral mechanism.
JOSHI, A. C. 1938. The nature of the ovular stalk in Polygonaceae and some related families. Ann. Bot. (N.S.) **2:** 957–959.
————. 1947. The morphology of the gynaeceum. Presidential Address Bot. Sect., Indian Sci. Cong. 34th Session, Part II, Delhi, 1-18.
JUNELL, S. 1934. Zur Gynöceummorphologie und Systematik der Verbenaceen und Labiaten. Symb. Bot. Uppsaliensis **4:** 1–219.
KIRKWOOD, J. E. 1905. The comparative embryology of the Cucurbitaceae. N. Y. Bot. Gard., Bull. **3:** 313–402.
KRATZER, J. 1918. Die verwandschaftlichen Beziehungen der Cucurbitaceen. Flora **110:** 278.
LAM, H. J. 1948*a*. Classification and the new morphology. Acta Biotheoretica **8:** 107–154.
————. 1948*b*. A new system of the Cormophyta. Blumea **6:** 282–289.
————. 1950. Stachyospory and phyllospory as factors in the natural system of the Cormophyta. Svenska Bot. Tidskr. **44:** 517–534.
LANGDON, LA DEMA MARY. 1939. Ontogenetic and anatomical studies of the flower and fruit of the Fagaceae and Juglandaceae. Bot. Gaz. **101:** 301–327.
LAUBENGAYER, R. A. 1937. Studies in the anatomy and morphology of the polygonaceous flower. Am. Jour. Bot. **24:** 329–343.
LAWRENCE, JULIA RUTH. 1937. A correlation of the taxonomy and the floral anatomy of certain of the Boraginaceae. Am. Jour. Bot. **24:** 433–444.
LE MAOUT, E. and DECAISNE, J. 1876. A general system of botany, descriptive and analytical. [Eng. trans. by Mrs. Hooker].

LEINFELLNER, W. 1950. Der Bauplan des synkarpen Gynöceums. Österr. Bot. Zeit. **97:** 403–436.
————. 1951. Die U-formige Plazenta als der Plazentationstypus der Angiosperms. Österr. Bot. Zeit. **98:** 338–358.
LINDLEY, J. 1830. An introduction to the natural system of botany.
————. 1847. The vegetable kingdom. 2nd Ed.
LINDSEY, A. A. 1940. Floral anatomy in the Gentianaceae. Am. Jour. Bot. **27:** 640–652.
LISTER, G. 1884. On the origin of placentae in the tribe Alisineae of the Order Caryophyllaceae. Jour. Linn. Soc., Bot. **20:** 423.
MAGNUS, P. 1869. Zur Morphologie der Gattung *Najas* L. Bot. Zeit. **27:** 769–773.
————. 1894. Ueber die Gattung *Najas*. Ber. Deut. Bot. Ges. **12:** 214–224.
NICOLOFF, TH. 1904–1905. Sur le type floral et le dévéloppement du fruit des Juglandées. Jour. de Bot. **18:** 134–152, 380–385; **19:** 63–84.
MANNING, W. E. 1938. The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruits. Am. Jour. Bot. **27:** 839–852.
————. 1940. The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruits. Am. Jour. Bot. **35:** 606–621.
MOSS, C. E. 1920. The Cambridge British Flora. Vol. 3.
MOTTIER, D. M. 1932. A textbook of botany for college students.
MURRAY, MARY ALLEEN. 1945. Carpellary and placental structure in the Solanaceae. Bot. Gaz. **107:** 243–260.
MURTY, Y. S. 1952. Placentation in *Peperomia*. [In press].
NAST, CHARLOTTE G. 1935. Morphological development of the fruit of *Juglans regia*. Hilgardia **9:** 345–362.
———— and BAILEY, I. W. 1945. Morphology and relationships of *Trochodendron* and *Tetracentron*. II. Inflorescence, flower and fruit. Jour. Arn. Arb. **26:** 265–276.
———— and ————. 1946. Morphology of *Euptelea* and comparison with *Trochodendron*. Jour. Arn. Arb. **27:** 186–192.
NEWMAN, I. V. 1928. The life history of *Doryanthes excelsa*. Proc. Linn. Soc. New South Wales **53:** 499–538.
PALSER, B. F. 1951. Studies of floral morphology in the Ericales. I. Organography and vascular anatomy of the Andromedeae. Bot. Gaz. **112:** 447–485.
PAYER, J. B. 1857. Traite d'organogenie comparee de la fleurs.
PLANTEFOL, L. 1849. L'ontogenie de la fleur.
POOL, R. J. 1940. Basic course in botany.
PRANTL, K. 1897. An elementary text-book of Botany. [Trans. by S. H. Vines].
PRIESTLEY, J. H. and SCOTT, LORNA I. 1949. An introduction to botany.
PURI, V. 1939. Studies in the order Parietales. II. A contribution to the morphology of *Garcinia livingstoni* T. Anders. Proc. Ind. Acad. Sci. **9:** 74–86.
————. 1941. Studies in floral anatomy. I. Gynaeceum constitution in the Cruciferae. Proc. Ind. Acad. Sci. **14:** 166–187.
————. 1942. Studies in floral anatomy. II. Floral anatomy of the Moringaceae with special reference to gynaeceum constitution. Proc. Nat. Inst. Sci. India **8:** 71–88.
————. 1945. Studies in floral anatomy. III. On the origin and orientation of placental strands. Proc. Nat. Acad. Sci. [India] **15:** 74–91.
————. 1947. Studies in floral anatomy. IV. Vascular anatomy of the flower of certain species of the Passifloraceae. Am. Jour. Bot. **34:** 562–573.

————. 1950. Studies in floral anatomy. VI. Vascular anatomy of the flower of *Crataeva religiosa* with special reference to the nature of the carpels in the Capparidaceae. Am. Jour. Bot. **37:** 363–370.
————. 1950*a*. Placentation in angiosperms. Proc. VII. Int. Bot. Cong., Stockholm.
————. 1951. The role of floral anatomy in the solution of morphological problem. Bot. Rev. **17:** 271–353.
————. 1952*a*. Studies in floral anatomy. VII. On placentation in certain species of the Cucurbitaceae. [In press].
————. 1952*b*. The flower. III. Placentation in the Rhoeadalean flower. Agra Univ. Extension Lecture. 1952.
RAGHAVAN, T. S. 1939. Studies in the Capparidaceae. IV. Floral anatomy and some structural features of the Capparidaceae. Jour. Linn. Soc. [London] **52:** 239–257.
———— and VENKATASUBBAN, K. R. 1941. Studies in the Capparidaceae. VII. The floral morphology of *Crataeva religiosa*. Proc. Ind. Acad. Sci. **13:** 235–243.
RAO, L. N. 1942. Studies in the Santalaceae. Ann. Bot. (N. S.) **6:** 151–175.
RASTOGI, S. P. 1951. Vascular anatomy of the flower of certain species of the Myrtaceae. [Unpubl. thesis. Agra Univ.]
RENDLE, A. B. 1938. Classification of flowering plants. Vol. II.
RENSCH, B. 1934. Kurze Anweisung für zoologisch-systematische Studien.
REUTER, K. 1926. Die Phylogenie der Parietales. Bot. Archiv. **36:** 118–217.
SACHS, J. 1882. Text-book of botany. [Engl. trans. by Vines, H. S.]
SAINT-HILAIRE, A. DE. 1816. Mémoire sur les plantes aux quelles on attribue un placenta central Libre.
————. 1847. Leçons de botanique.
SATINA, SOPHIE and BLAKESLEE, A. F. 1943. Periclinal chimeras in *Datura* in relation to the development of the carpel. Am. Jour. Bot. **30:** 453–462.
SAUNDERS, E. R. 1931. Illustrations of carpel polymorphism. VII. New Phyt. **30:** 80–118.
————. 1936. Some morphological problems presented by the flower in the Nymphaeaceae. Jour. Bot. **74:** 217–221.
SCHAEPPI, H. J. 1937. Vergleichend-morphologische Untersuchungen am Gynaeceum der Primulaceen. Zeit. Ges. Naturw. **3:** 239–250.
————. 1942. Morphologische und entwicklungsgeschichtliche Untersuchungen an den Blüten von *Thesium*. Mitt. Naturwiss. Ges. Winterthur **23:** 41–61.
———— und STEINDL, F. 1937. Blütenmorphologische und embryologische Untersuchungen an *Osyris alba* L. Ber. Schweiz. Bot. Ges. **47:** 369–392.
———— und ————. 1942. Blütenmorphologische und embryologische Untersuchungen an Loranthoideen. Viertel. Nat. Ges. Zurich **87:** 301–372.
———— und ————. 1945. Blütenmorphologische und embryologische Untersuchungen an einigen Viscoideen. Viertel. Nat. Ges. Zurich **90:** 1–46.
SCHENK, A. 1884. Handbuch der Botanik. Vol. III.
SCHLEIDEN, M. J. 1849. Principles of scientific botany. [Transl. by E. Lankester].
SCHUSTER, J. 1910. Über die Morphologie der Grasblüte. Flora **100:** 252.
SHUHART, D. V. 1932. Morphology and anatomy of the fruit of *Hicoria pecan*. Bot. Gaz. **93:** 1–20.
SINNOTT, E. W. 1946. Botany: principles and problems, 4th Ed.
———— and BAILEY, I. W. 1914. Investigations on the phylogeny of angiosperms. II. Bot. Gaz. **58:** 36–60.

SMITH, F. H. and SMITH, ELIZABETH C. 1942*a*. Anatomy of the inferior ovary of *Darbya*. Am. Jour. Bot. **29**: 464–471.
———— and ————. 1942*b*. Floral anatomy of the Santalaceae and related forms. Oregon State Mon. Bot. 5.
SMITH, G. H. 1928. Vascular anatomy of Ranalian flowers. II. Ranunculaceae (Contd.), Menispermaceae, Calycanthaceae, Anonaceae. Bot. Gaz. **85**: 152–177.
SPRATT, E. R. 1932. The gynaeceum of the family Cruciferae. Jour. Bot. **70**: 308–344.
SPROTTE, K. 1940. Untersuchungen über Wachstum und Nervatur der Fruchtblätter. Bot. Arch. **40**: 463–506.
STRASBURGER, E. 1879. Die Angiospermen und die Gymnospermen.
SWAMY, B. G. L. and BAILEY, I. W. 1949. The morphology and relationships of *Cercidiphyllum*. Jour. Arn. Arb. **30**: 187–210.
THOMAS, H. H. 1931. The early evolution of the angiosperms. Ann. Bot. **45**: 647–672.
THOMSON, BETTY FLANDERS. 1942. The floral morphology of the Caryophyllaceae. Am. Jour. Bot. **29**: 333–349.
THOMPSON, J. MCL. 1934. Studies in advancing sterility. VII. The state of flowering known as angiospermy (with special reference to placentation and the origin and nature of follicles and achenes. Univ. Liverpool, Hartley Bot. Lab., Pub. **72**: 47.
TIAGI, B. 1951. Studies in the family Orobanchaceæ. III. A contribution to the embryology of *Orobanche cernua* Loeffl. and *O. aegyptiaca* Pers. Phytomorph. **1**: 158–169.
TREVIRANUS, L. C. 1838. Physiologie der Gewachse. Vol. 2: 333. [Quoted from Huisgen, 1873].
TROLL, W. 1928. Organization und Gestalt im Bereich der Blüte.
————. 1939. Die morphologische Natur der Karpelle. Chron. Bot. **5**: 38–41.
————. 1948. Allgemeine Botanik.
URQUHART, BETTY A. 1943. The floral development and vascular anatomy of *Lycium halimifolium*. [Unpubl. Thesis, Univ. Chicago].
VAN TIEGHEM, PH. 1869*a*. Anatomie de la fleur femelle et du fruit du noyer. Bull. Soc. Bot. France **16**: 412–420.
————. 1869*b*. Anatomie de la fleur des Santalacées. Ann. Sci. Nat. V. Bot. **12**: 340–346.
————. 1869*c*. Structure de pistil des Primulacées et des Theophrastées. Ann. Sci. Nat. V. Bot. **12**: 329–339.
————. 1871. Recherches sur la structure du pistil et sur l'anatomie comparée del la fleur. Mem. Savants étrangers à l'Inst. II. **21**: 1–261.
————. 1891. Traité de botanique.
————. 1900. Sur les dicotylédones du groupe des Homoxylées. Jour. de Bot. **14**: 259–297; 330–361.
————. 1907. Structure du pistil et du fruit des Labiées, des Boragacées et des familles voisines. Ann. Sci. Nat. IX, Bot. **5**: 321–350.
VINES, S. H. 1896. A student's text-book of botany.
VIDAL, L. 1900. Recherches sur le sommet de l'axe dans la fleur des Gamepétales. Thesis, Paris.
VUILLEMIN, P. 1926. Les anomalies végétales.
WARMING, M. E. 1878. De l'ovule. Ann. Sci. Nat. VI. Bot. **5**: 177–266.
———— and POTTER, M. C. 1932. A handbook of systematic botany. Sec. Ed.
WARNER, E. 1933. The floral development and vascular anatomy of the flower of *Lycopersicum esculentum* var. *cerasiformis*. [Unpub. Thesis, Univ. Chicago.]
WEIBEL, R. 1945. La placentation chez les Tiliacées. Candollea **10**: 155–177.

WETTSTEIN, R. 1935. Handbuch der systematischen Botanik. Vol. 2.
WIGER, J. 1935. Embryological studies on the families Buxaceae, Meliaceae, Simarubaceae und Burseraceae. Thesis, Lund.
WILLIS, J. C. 1948. Dictionary of flowering plants and ferns. 6th Rev. Ed.
WILKINSON, A. M. 1944. Floral anatomy of some species of *Cornus*. Bull. Torrey Bot. Club **71:** 276–301.
————. 1948*a*. Floral anatomy and morphology of some species of the tribe Lonicereae of the Caprifoliaceae. Am. Jour. Bot. **35:** 261–271.
————. 1948*b*. Floral anatomy and morphology of some species of the tribe Linnaeeae and Sambuceae of the Caprifoliaceae. Am. Jour. Bot. **35:** 365–371.
————. 1948*c*. Floral anatomy and morphology of some species of the genus *Viburnum* of the Caprifoliaceae. Am. Jour. Bot. **35:** 455–465.
————. 1949. Floral anatomy and morphology of *Triosteum* and of the Caprifoliaceae in general. Am. Jour. Bot. **36:** 481–489.
WILSON, C. L. and JUST, T. 1939. The morphology of the flower. Bot. Rev. **5:** 97–131.
———— and X. 1947. Flower *In* Encyclopaedia Britannica.
WINKLER, H. 1941. Verstehen wir das Gynöceum der Angiospermen schon? Beitr. Biol. Pflanzen **27:** 242–267.
WOOD, A. 1845. A class-book of botany.
WOODSON, R. E., JR. and MOORE, J. A. 1938. The vascular anatomy and comparative morphology of the apocynaceous flower. Bull. Torrey Bot. Club **65:** 135–166.
WORSDELL, W. C. 1904. The structure and morphology of the "ovule". Ann. Bot. **18:** 57–86.
ZIMMERMANN, W. 1930. Die Phylogenie der Pflanzen.

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